In a globally changing climate, the question of whether (and how fast) species can adapt to alterations in their ecosystems has become a matter of major importance. The investigation of the endogenous (density-dependent) and exogenous (density-independent) processes that regulate population dynamics and thus determine the prospective trajectory of populations can provide valuable answers to these questions. In this thesis, I experimentally assess population responses to environmental (biotic and abiotic) conditions through the study of individual life-histories in order to reveal the underlying mechanisms of population regulation, using a vertebrate ectotherm with known ecological plasticity, the common lizard (*Zootoca vivipara*), as a model species.
As a species from a vulnerable taxon, the here presented results could help improve our predictive capacity concerning natural population responses of species at higher risk against future environmental changes and thus improve the effectiveness of the ongoing efforts to conserve biodiversity.

IPE
Instituto Pirenaico de Ecología
mncn
CSIC
Consejo Superior de Investigaciones Científicas
UAM
Universidad Autonoma de Madrid

Environmental Determinants of Population Dynamics of *Zootoca vivipara*

2016

Environmental Determinants and Mechanisms of Population Dynamics

Biotic and abiotic effects on life-histories of age-structured populations of common lizards (*Zootoca vivipara*)

Tesis doctoral
Cristina Romero Díaz
Museo Nacional de Ciencias Naturales
Madrid, 2016

MUSEO NACIONAL DE CIENCIAS NATURALES
(Consejo Superior de Investigaciones Científicas)
Dpto. de Biodiversidad y Biología Evolutiva

UNIVERSIDAD AUTÓNOMA DE MADRID
Facultad de Ciencias
Dpto. de Biología

ENVIRONMENTAL DETERMINANTS AND MECHANISMS OF POPULATION DYNAMICS:

BIOTIC AND ABIOTIC EFFECTS ON LIFE-HISTORIES OF AGE-STRUCTURED POPULATIONS OF COMMON LIZARDS (*ZOOTOCA VIVIPARA*)

Memoria presentada por la licenciada Cristina Romero Díaz para optar al Grado de Doctora en Biología por la Universidad Autónoma de Madrid.

DIRECTOR:

Patrick S. Fitze
Museo Nacional de Ciencias Naturales
Dpto. de Biodiversidad y Biología Evolutiva
Madrid

TUTOR ACADÉMICO:

Fco. Javier de Miguel Águeda
Universidad Autónoma de Madrid
Dpto. de Biología
Madrid

TESIS DOCTORAL
Madrid, 2016

<< No book reviewing an area of active research should give the impression that everything has been done >>

(S. C. Stearns)

Contents

Acknowledgements

Esta tesis va en primer lugar dedicada a los que han estado, están y siempre estarán en mi vida: a los Romero Díaz. Dicen que uno elige a sus amigos, pero no a su familia. Si me hubieran dado a elegir, no habría querido nacer en ningún otro lugar. Siempre me he sentido afortunada y por ello, agradecida. Así que una vez más, gracias. Gracias por crear un hogar en el que poder ser yo misma, perseguir mis sueños y vivir mi vida con la libertad que existe cuando se es consciente del apoyo que hay detrás. Gracias por educar con el ejemplo de lo que significa ser humano y mejor persona. En definitiva, gracias por tener empatía y principios en un mundo aparentemente caótico, con desperfectos, a veces falto de sensibilidad. Mamá, Papá, Carlos, Marcos, os quiero. Sin vuestro apoyo esta tesis, literalmente, no se habría terminado.

A mi extensa familia, dentro y fuera de "Eventos", me gustaría también darle las gracias, por seguir el día a día de los quehaceres de unos y otros de forma tan sincera y cercana. A mis tías Paloma y Chari, les agradezco de corazón su implicación y esfuerzo en los momentos difíciles de este último año y medio. A mi padrino Jose, y a Ángeles, les agradezco haber tenido siempre especial interés en los pasos que iba dando mi vida. A la inolvidable e inigualable abuela Angelines, ejemplo de lo que significa tener éxito en la vida, perdóname por no haber podido despedirme en persona.

A mi "familia inclusiva", formada por mis compañeros de fatigas y de trabajo a los que tengo el orgullo de llamar amigos, con quienes he podido compartir mi pasión por esta forma de vida que es la biología, y no se me ocurren mejores personas: Miguel y Merel, simplemente gracias por todos los momentos compartidos. A Luis y a Virginia, gracias por todo lo enseñado. A los compañeros de despacho, permanentes o temporales, inmersos en sus respectivas batallas, gracias por hacer el camino menos solitario y sin duda más agradable: Paloma, Guille, Alfonso, Sofía, Javi, Patri y en general al ecléctico Depto. de Biodiversidad y Biología Evolutiva del MNCN, estudiantes e investigadores, ¡cuánta buena gente en tan poco espacio! Gracias a Mario García por amenizar muchas tardes con cenas en casa, a Rodrigo por su entusiasmo contagioso y la oportunidad de 'campear' lagartijas, que al final es lo que nos gusta más hacer, y a Marcos por su filosofía desenfadada sobre la vida y nuestra profesión.

Gracias a Patrick S. Fitze por construir y financiar un ambicioso e interesante proyecto de investigación en el que comenzar mi andadura como bióloga. También a Rafael Zardoya por su apoyo en momentos importantes. Gracias a Borja Milá y a Marta Barluenga por sus sabios consejos y por su amistad, han significado mucho para mí. A Javier de Miguel, mi tutor en la Universidad, por su siempre buena disposición y ayuda. A la gente del Instituto Pirenaico de Ecología en Jaca, por darnos un espacio entre los suyos durante los largos periodos que pasamos en el campo, y a María Urieta, mis mejores deseos.

Thank you to the former and current members of Journal Club (and thank you Marta for leading it all these years), it has been a pleasure.

Gracias también a mi más fiel lector, David, por renovar su suscripción anual al *newsletter* de mi vida. A los ajenos a este mundo de "locos ecologistas", mi más *viejo* amigo Juan Antonio, y a Nico al otro lado del océano por no perder el contacto. To those of you abroad, I have only good memories to cherish; Rudito, the sweetest soul ever, I'm glad we could meet. Very special thanks to Hanna (and the kokkonuts!) for her warmth, her good-naturedness and all her always constructive input; you have taught me a lot, in and out of science. To Allison Shaw for making the Canberra experience even better; Luke Holman, Tonya Haff and Rob Lanfear for taking me in their home while I was so far from my own. Thanks to Lisa Schwanz for a fantastic field-work opportunity, and the rest of the "Australian bunch" including Scott Keough, Mike Jennions, and Janet Elliott at the Division of Evolution, Ecology and Genetics at ANU. You are a welcoming lot. Thank you all!

Para terminar, la investigación de esta tesis no habría sido posible sin los fondos de los proyectos y organizaciones referidos en los agradecimientos de cada capítulo y los permisos concedidos por la administración. El Ministerio de Educación, Cultura y Deporte financió mi trabajo durante 4 años con una Beca FPU, y varios Proyectos del Plan Nacional de I+D+i y la Swiss National Science Foundation concedidos a P. S. Fitze financiaron los experimentos.

FOREWORD

The ultimate objective of all conservation efforts is to preserve diversity (i.e., variability) at different levels of biological and ecological organization. Variability among individuals of a species is required for natural selection to occur, and thus the evolutionary processes responsible for the global biodiversity that we observe today could not have happened in its absence. It has long been recognized that intra-specific variability can facilitate adaptation to naturally variable environments and thus favor the persistence of species over time. Adaptation can be achieved through phenotypic plasticity—the ability of a single genotype to produce different phenotypes in alternative environments—or through changes in the genetic composition of populations via selection, a process that can be more or less slow, depending on each species' biology.

In a globally changing climate, the question of whether (and how fast) species can adapt to alterations in their ecosystems, especially those of anthropogenic origin, has become of paramount importance. To answer this question, we must first know how species respond *in situ* to environmental change (adaptive capacity), and to what extent they are affected by those changes (sensitivity). Such knowledge can be used to improve management of conservation efforts and aid the preservation of biodiversity. Climatic patterns are predicted to change at unprecedented speed in recent history, bringing novel climates to most land areas to which organisms are not *a priori* adapted and consequently, an increase in extinction risk is likely to result. Current bioclimatic models aiming to predict future species distributions in response to climate change (and thus their persistence or extinction) give projections that can be very variable and their predictions may fail, among other things, due to inaccurate ecological assumptions. More importantly, their predictions do not necessarily rely on causality between environmental conditions and distributions, and, in truth, little is known about the proximate causes of climate-change related extinctions. This gap could be bridged with manipulative studies (experiments) on potential proximate causes of population decline, which entail the assessment of cause-effect relationships between biotic or abiotic factors and the local dynamics of populations, and with the improvement of our knowledge on species biology (e.g., environmental tolerances).

There exists a close relationship between individual fitness (roughly, survival and reproduction), demographic features of populations and density-independent (i.e., exogenous) factors, which connect through individual life-histories. At the individual

level, the study of life-history traits can help us understand the vulnerability of a species to environmental alterations and the action of selective pressures that shape population dynamics, which in turn determine their prevalence or extinction. Thus, life-history theory constitutes an appropriate framework to understand the action and mechanisms of natural selection operating on populations under different environments.

The aim of this thesis project was to experimentally assess population responses to environmental (biotic and abiotic) conditions through the study of individual life-histories, revealing relationships of causation, and explore the proximate mechanisms involved using as a model species a vertebrate ectotherm with known ecological plasticity, the common lizard (*Zootoca vivipara*).

PRESENTACIÓN

El objetivo final de todos los esfuerzos conservacionistas es preservar la diversidad (i.e., variabilidad) a diferentes niveles de organización biológica y ecológica. La variabilidad entre los individuos de una especie es necesaria para que la selección natural actúe, y por lo tanto, los procesos evolutivos responsables de la biodiversidad global que observamos hoy no podrían haber ocurrido en su ausencia. Durante mucho tiempo ha sido reconocido que la variabilidad intra-específica puede facilitar la adaptación a ambientes naturalmente variables y por lo tanto favorecer la persistencia de las especies a lo largo del tiempo. La adaptación puede lograrse a través de la plasticidad fenotípica—la capacidad de un solo genotipo para producir diferentes fenotipos en diferentes ambientes—o mediante cambios en la composición genética de las poblaciones a través de selección, un proceso que puede ser más o menos lento, dependiendo de la biología de cada especie.

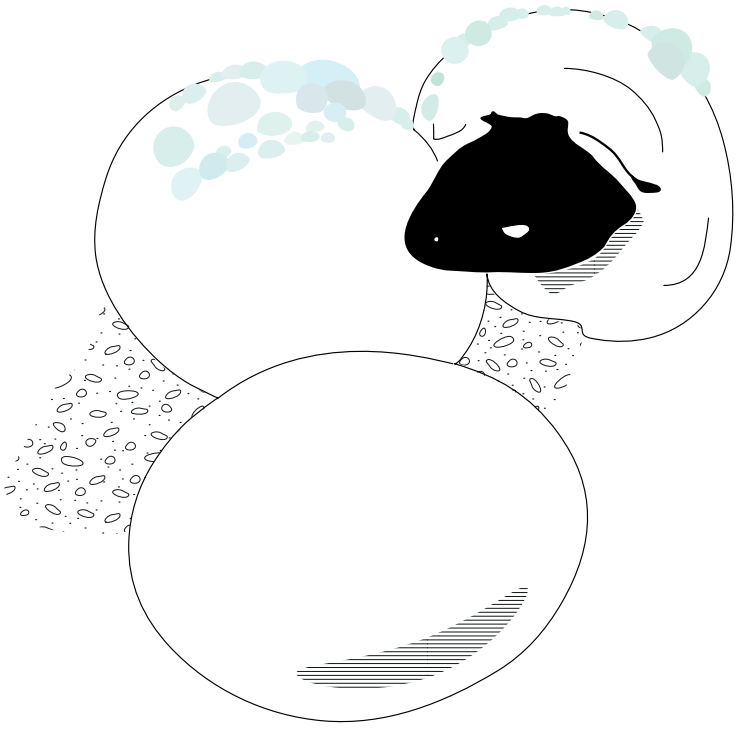
Ante un clima global cambiante, la cuestión de si (y cómo de rápido) las especies pueden adaptarse a las alteraciones de los ecosistemas, especialmente aquellas de origen antropogénico, ha adquirido suma importancia. Para responder a esta pregunta, primero debemos saber cómo responden las especies a los cambios ambientales y en qué medida se ven afectadas por dichos cambios. Este conocimiento puede ser utilizado para mejorar la gestión de los esfuerzos conservacionistas y ayudar a la preservación de la biodiversidad. Está previsto que los patrones climáticos cambien a una velocidad sin precedentes en la historia reciente, trayendo nuevos climas a la mayor parte de las áreas terrestres, a los cuales los organismos no están adaptados y, en consecuencia, es probable que se produzca un aumento del riesgo de extinción. Los modelos bioclimáticos actuales destinados a predecir los efectos del futuro cambio climático en la distribución de las especies (y por tanto su persistencia o extinción) dan proyecciones que pueden ser muy variables y/o predicciones que pueden fallar, entre otras cosas, debido a supuestos ecológicos inexactos. Más importante aún, dichas predicciones no se apoyan necesariamente en relaciones de causalidad entre condiciones ambientales y distribución, con lo que en realidad, se sabe más bien poco sobre las causas próximas de las extinciones relacionadas con el cambio climático. Esta brecha podría ser salvada con estudios basados en la manipulación (experimentos) de las posibles causas inmediatas de declive poblacional, que implican la evaluación de relaciones causa-efecto entre factores bióticos o abióticos y la dinámica poblacional a

nivel local, y también con la mejora de nuestro conocimiento sobre la biología de las especies (p. ej., sus tolerancias ambientales).

Existe una estrecha relación entre la eficacia biológica individual (a grandes rasgos, la supervivencia y reproducción), factores independientes de la densidad (i.e., exógenos) y los parámetros demográficos de las poblaciones, conectados a través de las historias vitales individuales. A nivel individual, el estudio de los rasgos de las historias vitales puede ayudarnos a entender la vulnerabilidad de una especie frente a alteraciones ambientales así como la acción de las presiones de selección sobre la dinámica poblacional que, a su vez, determinan su prevalencia o extinción. Por ello, la teoría en torno a las historias vitales constituye un marco adecuado para entender la acción y los mecanismos de la selección natural que operan en las poblaciones bajo diferentes ambientes.

El objetivo de este proyecto de tesis es evaluar experimentalmente las respuestas poblacionales frente a condiciones ambientales (bióticas y abióticas) a través del estudio de las historias vitales individuales, poniendo de manifiesto relaciones de causalidad, y explorar los mecanismos próximos implicados, utilizando como especie modelo un vertebrado ectotermo con conocida plasticidad ecológica, la lagartija de turbera (*Zootoca vivipara*).

General Introduction



Populations and conservation

The individuals of a species can be found distributed over a wide geographical range, at times inhabiting different biogeographical regions within different continents (Sclater 1858; Wallace 1876). At a larger scale, a group of individuals of the same species occupying a specific area at a certain time, capable of interbreeding, constitute a *population* (Chapman and Reiss 1998). Thus, species are composed of a number of populations among and within which *variability* may exist. Populations are characterized by demographic features, mainly, the number of individuals (size and density), the age structure and sex ratio, and by demographic rates: births, deaths, immigration, and emigration (Chapman and Reiss 1998). The changes in the demographic features of populations are ultimately determined by changes in demographic rates, which are directly linked to the main events and processes of individual life cycles (e.g., reproduction, growth rates, mortality; Dublin and Lotka 1925; Steiner et al. 2014).

Population dynamics (also, demography) follow the changes in the size and demographic rates of biological populations over time and/or space (Chapman and Reiss 1998). We could roughly consider this as the "behavior" of populations. In turn, the broader field of *population ecology* is concerned with how populations interact with the environment and how this affects population dynamics. In nature, different population dynamic patterns can be observed, ranging from the simplest case of a population strongly regulated around a stable equilibrium at one end, to random population growth/decline at the other (Cappuccino and Price 1995). Commonly, populations are in a state of balance achieved by regular oscillations around an average density (i.e., following periodic cycles; Kendall et al. 1998; Nicholson 1954).

The study of population ecology is pivotal in *conservation biology* (Soulé 1985), a discipline that is most concerned with the planet's biodiversity and aims to preserve species and their ecosystems by determining the factors and causes of natural population declines (especially those of anthropogenic origin), and by developing proactive strategies to prevent extinctions (Caughley 1994; Primack 2004). In general, six categories of threats to biodiversity have been proposed: habitat loss and degradation, introduced invasive species, environmental pollution, disease and parasitism, unsustainable use (e.g., overexploitation), and global climate change (Gibbons et al. 2000; Primack 2004). More often than not, the decline of a species is the result of a cumulative effect of two or more of these problems, and there can exist

synergisms among threats (Sala et al. 2000). For example, the main effects of climate change on biodiversity are mediated through habitat changes in response to local weather parameters (IPCC 2013), which may aggravate the habitat degradation problem. In turn, changes in habitat conditions can facilitate the colonization of new areas by invasive species, or constitute environmental stressors that impair individual resistance to disease or parasites (Gibbons et al. 2000).

Recent studies suggest that climate change will become the major global threat to biodiversity in the coming decades of the 21st century, even surpassing habitat loss (IPCC 2014b; Leadley et al. 2010). Projections from models of virtually all available scenarios of CO_2 emissions for the future agree in a general trend of "further warming and changes in all components of the climate system" with variation in their magnitude (IPCC 2013), including alterations on components of temperature, precipitation, and drought (see Table 1.1). However, assessing changes in biodiversity as a consequence of climate change is a complicated task due to biotic uncertainties and statistical limitations of the available methodologies (Araújo and Rahbek 2006; Dawson et al. 2011; IPCC 2013), largely based on species distribution models (SDMs; Guisan and Thuiller 2005). SDMs such as "empirical niche" or "climate-envelope" models are built on correlative relationships between current (or past, in the case of paleoclimatic models) environmental climatic variables and current (or past) geographic patterns of species distributions. Among biotic uncertainties, incomplete surveys or data records on species distributions, potentially simplistic ecological assumptions, and failure to capture the biological idiosyncrasies of different species can impair the accuracy of future predictions and incur in high variability among projections from alternative models (Bellard et al. 2012; Keenan et al. 2011). Despite these drawbacks, the vast majority of published studies implementing modeling tools, including those with the most conservative approaches (e.g., consensus models, averaging projections; Araújo et al. 2005; Thuiller 2004), support the causal attribution to climate change of the observed biological trends on species and ecosystems across the globe (Araújo et al. 2006; Bellard et al. 2012; Jiguet et al. 2007; Parmesan 2006; Parmesan et al. 2000; Parmesan and Yohe 2003; Sinervo et al. 2010; Walther et al. 2002). In sum, the consensus about the role of climate change in the current and future loss of biodiversity is substantially robust.

In the face of current and future climatic change, conservationists are increasingly concerned about the impacts of weather-related change on virtually all levels of biodiversity, from organisms to biomes (Figure 1.1). The *vulnerability* of a species to the

Table 1.1 Summary of projected changes on the most relevant climatic components for the 21st century. Details on the direction/trend of the change, the region of the planet or specific season, and references from the literature are provided.

Climatic event Component	Direction/trend	Where /when	References
Temperature			
Mean	increase	global	(Easterling et al. 2000; IPCC 2013)
Extremes (min/max)	increase	global	(Easterling et al. 2000; IPCC 2013)
Precipitation			
Mean	increase (decrease) [locally variable]	overall, mid-latitude wet regions (tropics, dry regions, in summer)	(Dai 2011; Easterling et al. 2000; Gregory et al. 1997; IPCC 2013; Sun et al. 2007; Trenberth et al. 2003)
Extremes (heavy precipitation events)	increase intensity and frequency	global, wetter regions/ during summer	(Allan and Soden 2008; Easterling et al. 2000; Groisman et al. 1999; IPCC 2013; Sun et al. 2007)
Drought			
Intensity/Frequency	increase	drier regions, overall, Western Europe	(Allan and Soden 2008; Arnell 1999; Dai 2011; Easterling et al. 2000; IPCC 2013)
Duration	increase	global	(Easterling et al. 2000; IPCC 2013)
Atmosphere water vapor	increase (decrease) [depends on rain patterns]	wet regions, (snow dominated regions of N. Hemisphere)	(Barnett et al. 2005; Dai 2011; Wentz et al. 2007)
Sea level	rise	global	(IPCC 2013)
Ice cover			
Sea ice caps	shrink	the Arctic region and Antarctica	(IPCC 2013)
Glaciers, permafrost, snow cover	decrease	global, high northern latitudes, lowlands and Eastern Europe/ earlier in spring	(Arnell 1999; Barnett et al. 2005; IPCC 2013)

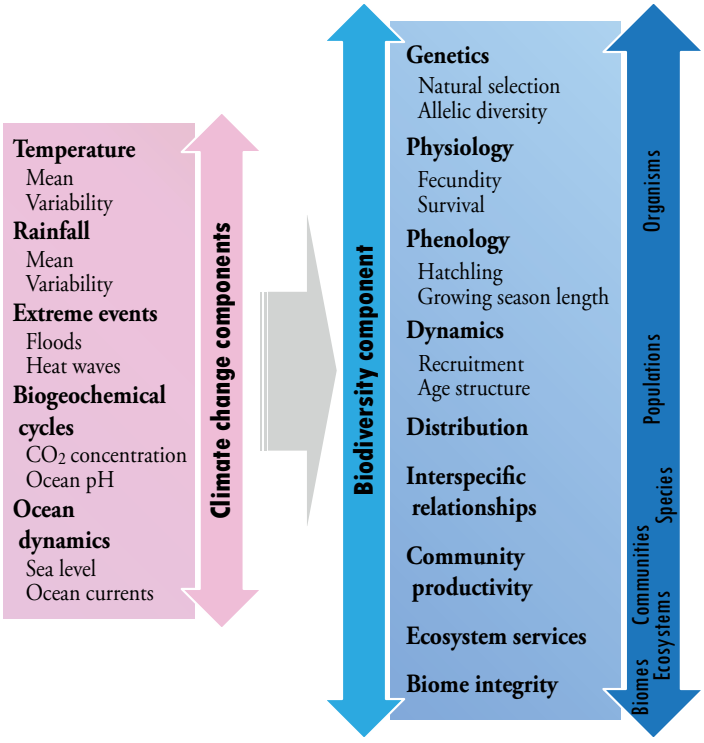


Figure 1.1 Likely effects of climate change components (left) on different levels of biodiversity (right), from individual organisms (above) to biomes (below), with particular examples in aspects of organisms and populations. Adapted from Bellard et al. 2012.

effects of climate change, this is, its propensity to be adversely affected (IPCC 2014b), is not only a matter of *exposure*. Exposure refers to the presence of species in places and habitats that could be negatively affected by climate change and thus it determines the likelihood of experiencing its impacts. SDMs are useful tools to assess exposure but practically do not consider *sensitivity* or *adaptive capacity*, the other two dimensions of climate change vulnerability (Dawson et al. 2011; Foden et al. 2013; Pacifici et al. 2015). Sensitivity describes a species' susceptibility or tolerance to climatic variation and it depends on a variety of intrinsic factors, including physiological tolerances, ecological traits, and microhabitat specialization (Dawson et al. 2011; Foden et al. 2013; Williams et al. 2008). The adaptive capacity refers to a species' ability to cope with adverse impacts of climate change, either *in situ* or through dispersal and/or migration to more favorable areas, and depends on both intrinsic (e.g., phenotypic plasticity, genetic diversity, colonization ability) and extrinsic factors (e.g., magnitude and nature of climatic change; Dawson et al. 2011). Therefore, the combination of multiple, complementary approaches to SDMs, including e.g., paleoecological records, direct observations, experiments, and mechanistic models, is essential to take into

account all three aspects of vulnerability and achieve more accurate vulnerability and risk assessments (Bellard et al. 2012; Dawson et al. 2011; Keenan et al. 2011).

Among complementary approaches, mechanistic methods like population models and experimental manipulations are particularly recommended to assess aspects of sensitivity and adaptive capacity (e.g., Drake 2005; Knapp et al. 2002; Mearns et al. 1997). Unfortunately, at least in the last two decades, correlative approaches alone have remained the preferred option (Pacifici et al. 2015; Sinclair et al. 2010). Nevertheless, considerable effort has recently been dedicated to identify the gaps and limitations of current approaches (e.g., Bellard et al. 2012; Guisan and Thuiller 2005; McMahon et al. 2011; Sinclair et al. 2010) and to make recommendations to improve species vulnerability assessments, among which stand out:

1. **The need to study a wider range of species**. So far, studies have been limited to a small percentage of all known biodiversity and they have been biased geographically and taxonomically. While taxonomic groups of birds, mammals and plants have been particularly well studied, many others have been neglected (Bellard et al. 2012; Pacifici et al. 2015).
2. **The need to investigate species responses in terms of sensitivity and adaptive capacity.** Populations of many species are estimated to have the potential to respond via microevolution or via phenotypic plasticity to changing climate (Baker et al. 2004; Visser 2008). The limits of such capacity must be determined empirically to predict *in situ* ecological and evolutionary responses to environmental change (Dawson et al. 2011; Nicotra et al. 2015).
3. **The need to take into account dynamics that determine extinction risk at local scale.** This would increase the accuracy of predictions, but it also requires a deeper understanding of the ecological mechanisms acting at the inter-individual level that are responsible for a given population dynamic (e.g., Clutton-Brock and Coulson 2002).

In conclusion, more experimental studies on the individual level and demography are needed. The experimental manipulation of populations constitutes a fitting approach to address all three issues above, if applied to species from understudied taxonomic groups (Benton and Beckerman 2005). It can provide comprehensive information on the effects of environmental factors on the adaptive capacity of individuals and the mechanisms underlying dynamic processes (Beckerman et al. 2002; Nicotra et al. 2015).

From individual life-histories to the dynamics of populations

Individual organisms are the fundamental units of populations, as populations are the units of species (Chapman and Reiss 1998). While evolution occurs at the population level (Mayr 1998), it is individual organisms that are the product of natural selection (Darwin 1859). Lincoln et al. (1998) defined the term "*life history*" as "the significant features of the life cycle through which an organism passes, with particular reference to strategies influencing survival and reproduction". The phenotypic traits that describe an organism's life-history are thus called *life-history traits* and are closely related to individual *fitness,* i.e., an individual's contribution to the gene pool of the next generation relative to the contributions of other individuals (Darwin 1872; Haldane 1924). Some of the more relevant life-history traits are (Stearns 1992):

- Size at birth.
- Growth pattern.
- Age and size at maturity.
- Number, size, and sex ratio of offspring.
- Reproductive investment.
- Longevity.

Like many phenotypic traits, life-history traits have a tendency to vary among individuals in a population, thus differences in fitness among life-history variants may exist. The fitness of a particular life-history is closely linked to the intrinsic rate of increase (in size) for a population (Lande 1982). Since life-history theory seeks to explain how variation in life-history traits can lead to variation in fitness, it can help us understand the action of natural selection on individuals and therefore populations (Stearns 1992). The key steps are to identify the sources of, and constraints to life-history variation and to translate their effects into generally applicable relationships between life-history traits and population growth (Stearns and Koella 1986). The strong links between life-history traits, fitness and population dynamics, and their natural variability make individual life-histories crucial in understanding how individuals will respond to environmental change (Lessells 2008).

Currently, we can find two phenomenological approaches to the understanding of the mechanisms by which the environment affects individual life-histories and the dynamics of populations. On the one hand, the "top-down" approach (Benton and

Beckerman 2005) uses inference from population-level experiments to deduce the biological mechanism responsible for population dynamics. On the other hand, the "bottom-up" approach (Benton and Beckerman 2005) relies on the rationale presented above that environmental conditions cause changes in life-history traits of individual organisms, thereby changes in demographic rates, and ultimately population dynamics. In turn, changes on populations are likely to modify the interaction network at the community and ecosystem levels (Bellard et al. 2012; Rudolf and Rasmussen 2013; Walther 2010; see also Figure 1.1). The bottom-up approach offers insight into how individual strategies translate into higher-level changes that top-down approaches cannot provide (e.g., Benton and Beckerman 2005; De Roos et al. 2003). Consequently, if we want to explore the causes of variation in population dynamics, we must look into the mechanisms affecting the life-histories of individuals.

Life-histories in structured populations

In population biology, a distinction is made between "unstructured" and "structured" populations. In unstructured populations, demographic rates are considered roughly identical across individuals (e.g., a bacteria colony). However, in most cases this assumption is an oversimplification of reality, insofar as the individuals that make up populations differ in attributes such as size, age, ontogenetic development, physiological state, or their history of past experiences. This allows to group the individuals of a population according to classes or *stages*. Structured populations can be more or less complex, depending on the number of stages and the resulting diversity of interactions among individuals (Coulson and Godfray 2007). Unsurprisingly, structured populations are more challenging to describe for theoretic population ecologists and even though almost a century has passed since the modern resurgence of the field, the first population models to incorporate structures (other than discrete age) date back to a few decades ago, and the development of comprehensive models that describe and/or predict the changes of these populations is still ongoing (Caswell 2001; De Roos et al. 2003).

The importance of accounting for population structure when assessing the effects of environmental conditions on life-history traits resides in the ample ecological variation (e.g., diet, phenology, habitat use) that exists among different stages within the same species, which can even surpass the differences found between two different species (Rudolf and Rasmussen 2013; Trivers 1972). One of the largest sources of this inter-stage variation stems from differences in body size and developmental stage (e.g.,

allometry during ontogeny). Certain age or stage classes are typically more susceptible to perturbations than others and this is reflected in variances of individual reproductive rates and survival/mortality rates among stages (Coulson et al. 2001; Coulson and Godfray 2007; Steiner et al. 2014). For instance, it is common for the younger cohorts to exhibit greater mortality than adults and for reproductive performance to diminish with age after maturation (i.e., *reproductive senescence*; Nussey et al. 2013). Good examples of these phenomena have been documented in long-term population studies of mammals (Broussard et al. 2003; Clutton-Brock and Coulson 2002; Hayward et al. 2013), fish (May 1974), birds (Blums et al. 1996; Jovani and Tella 2004; Reed et al. 2008), reptiles (Massot et al. 2011; Miller et al. 2014; Richard et al. 2005) and insects (Bonduriansky and Brassil 2002). As a result, the structure composition of populations is disrupted, which can have important consequences for its dynamic, the functional configuration of their communities, and thus ecosystem processes (Coulson et al. 2001; Coulson and Godfray 2007; Rudolf and Rasmussen 2013). This suggests that natural ecosystems could be much more sensitive to perturbations than previously thought and emphasizes the importance of understanding how intra-population variation drives local scale dynamics.

Life-history variation

Because life-history traits are related to fitness, they are generally under considerable selection. Variation in life-history traits is thus affected by selection pressures that can act on them either directly and/or owing to indirect constraints (Stearns 1992). Taxonomic level analyses have shown that inter-specific life-history variation can have a large environmental component, even after correcting for patterns of covariation within phylogenetic families (i.e., variation due to common ancestry (Dunham and Miles 1985; Miles and Dunham 1992; Winemiller and Rose 1992). The same can be said about intra-specific variation, where differences in life-histories among individuals are not purely genotypic (Roff 1992; Stearns 1992).

In fact, an individual's phenotype is a combination of genes and the environment in which they are expressed (West-Eberhard 1989). As a result, during ontogeny the same genotype can produce alternative morphological, physiological, and behavioral phenotypes in different environments—ideally the fittest phenotype in each particular environment—a process that is known as *phenotypic plasticity* (Pigliucci 2005; Box 1.1) and adds a new dimension to inter-individual variation in life-history traits. The set of phenotypes produced by the same genotype across a range of environments is called a

reaction norm and describes the environment-phenotype function specific of a genotype (Figure I, Box 1.1). Phenotypic plasticity is considerably important for adaptation (DeWitt and Scheiner 2004) and almost all life-histories are phenotypically plastic. Take for instance the timing of reproductive events for an iteroparous, multivoltine, oviparous species during a reproductive season: when to lay a clutch, with how many eggs, and how many times are 'decisions' that vary tremendously among individuals (e.g., Bauwens 1999) and are certainly affected by the environmental conditions (Visser 2008; Visser et al. 2003). The fitness (e.g., offspring survival to breed) associated with each possible strategy can vary just as much and sometimes life-history patterns that reduce the fitness variance, or "bet-hedging strategies" (Slatkin 1974), are favored (Roff 1992; Stearns 1992).

Plasticity would be perfect if organisms could measure directly the components of the environment that determine the optimal trait phenotype and immediately respond

Box 1.1 | Reaction norms and plasticity

Any given phenotype (e.g., trait) is not plastic if it remains constant across a range of environments (e.g., G_1, Figure I); the steepness of the slope indicates how much plasticity exists in an individual. When the reaction norms of two alternative genotypes never cross (e.g., G_3 & G_4, Figure I), ineludibly one genotype is superior to the other across all environments. If the phenotype is a fitness trait, it will eventually be fixed in the population. Conversely, crossing (i.e., not parallel) reaction norms (e.g., G_2 & G_3 or G_2 & G_4, Figure I) whose relative competitiveness depends on the environmental conditions, are expected to be pervasive because, in this case, no genotype is always superior to the others (Stearns 1989). Crossing reaction norms reveal genotype × environment interactions (G × E). G × E may refer to either: 1) a phenotype as a result of ongoing interactions between genes and environments throughout the development at the individual level; or 2) genetic variation for the slope of the reaction norm at the population level (Pigliucci 2005). Reaction norms are not necessarily linear.

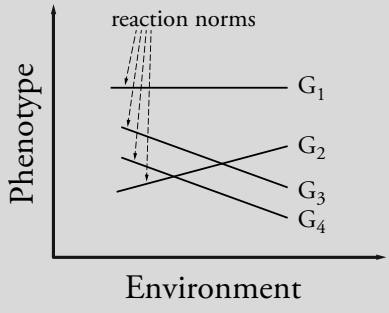


Figure I | Reaction norms of alternative genotypes (G). Slopes that differ from zero show different levels of individual plasticity. Crossing reaction norms depict genotype × environment interactions.

to adapt. However, the proximate external cues involved in the plasticity often differ from the variables that determine selection (e.g., because the latter are not available at the time) and environmental variables are only useful as cues if they are reliable, that is, if they accurately predict the future environment responsible for selection (Lancaster and Sinervo 2011; Shuster and Wade 2003; Visser 2008). On the other hand, plasticity has costs and limitations concerning the capacity for immediate change and the production of the optimal phenotype (Pigliucci 2005; Schlichting and Smith 2002; Snell-Rood et al. 2010) arising from information acquisition costs, lag-time limits to response, insufficient genetic variation, and physiological restrictions due to developmental modularity (level of integration), among others (DeWitt et al. 1998; Snell-Rood et al. 2010).

In summary, micro-evolutionary processes of local adaptation via selection, phenotypic plasticity to local environmental heterogeneity, and physiological constraints are likely to be important factors in shaping life-history variation (Dunham and Miles 1985). We can reunite the processes that introduce and affect variation in life-history traits among individuals in a population in two types (Flatt and Heyland 2011):

A. Environmental variation with age- or stage-specific effects.
B. Constraining trade-offs between connected life-history traits.

A. Environmental variation

Hardly any population grows indefinitely. In fact, for a real population to persist in the long term, demographic rates cannot remain constant (Coulson and Godfray 2007). There are a number of environmental factors acting on populations that influence population dynamics and whose effects are traditionally classified in two categories: *Density-dependent* (also known as endogenous or deterministic) and *density-independent* (also known as exogenous or stochastic) effects. Density-dependent effects are mediated through changes in population size (density) or structure of the current population, whereas density-independent effects are temporal and/or spatial fluctuations that affect the demographic rates of all individuals, independently of population size (Coulson and Godfray 2007). The most common types of density-independent effects are *demographic* and *environmental stochasticity* (Figure 1.2). Quite frequently, there will be interactions between density-independent and density-dependent effects that alter

the stability of the dynamic (Coulson et al. 2001; Sæther 1997), which is especially important in populations with more than one stable equilibrium and populations that do not settle on a stable equilibrium but show persistent cycles (Box 1.2).

Both biotic and abiotic factors can affect population growth directly or indirectly by influencing the frequency, extent, magnitude, or duration of one or more demographic processes (either in a density-dependent or -independent manner). Biotic factors include, among others, interactions of individuals either with members of their own species (e.g., intraspecific competition, crowding, cannibalism) or members of different species (e.g., interspecific competition, predation, mutualism, parasitism), population sex-ratio, or the species generation time. Competition in structured populations has the potential of becoming asymmetric among individuals from different stages, which can also lead to cyclical population oscillations (Box 1.2; De Roos and Persson 2003).

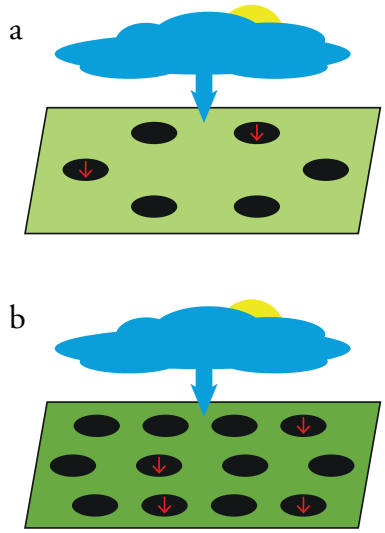


Figure 1.2 Illustration of density-dependent and density-independent effects in two unstructured populations differing only in size (a: n = 6; b: n = 12). Environmental stochasticity (e.g., weather) affects all individuals in the same way, irrespective of population size (blue arrow; a = b). Demographic stochastic effects, also independent of population size, result from fluctuations in probabilistic discrete events (e.g., by chance, some individuals suffer reduced reproductive rate; proportion of downward red arrows, a = b). In contrast, the magnitude of density-dependent effects (green color saturation) changes according to population density (e.g., competition; a < b).

Abiotic factors such as weather variables (e.g., precipitation, temperature, humidity) are important sources of environmental stochasticity (Stenseth et al. 2002; Figure 1.2). These interact with physiological mechanisms and introduce variation in values of phenotypic traits (Forchhammer et al. 2001), thus they also affect life-histories of individuals. In this manner, environmental stochasticity has a direct effect on the size and structure of the current population (i.e., a density-independent effect) and, at the same time, these changes in population density influence the future trajectory of the population (e.g., via density-dependent effects on life-history traits and, thereby, on the

Box 1.2 | Population cycles

Cyclic population dynamics are common in nature (Kendall et al. 1998). Classic theoretical ecology distinguished two types of cycles: cycles in which the fluctuation periodicity was slightly larger than the generation time of the individual, or "single generation cycles", and cycles where the fluctuation periodicity was at least twice as large than the generation time, or "delayed-feedback cycles" (Gurney and Nisbet 1985). Alternative mechanisms of competition were considered responsible for this dichotomy (Gurney and Nisbet 1985; Gurney et al. 1983). Today, it has been shown that both types of cycles can result from a single model, using a flexible time delay of the effect of competition. Thus, it is not possible to infer the exact mechanism of competition (i.e., the biological mechanism) acting in a population only from the oscillation period (Pfaff et al. 2014).

The original description of delayed-feedback cycles prompted an interest in the consequences of delayed life-history effects in population dynamics. Such effects may result, for example, when conditions during early development influence an individual or cohort's performance later in life (Beckerman et al. 2002) or when *maternal* (or paternal) *effects* (i.e., "the causal influence of the maternal genotype or phenotype on the offspring phenotype"(Wolf and Wade 2009) significantly influence offspring performance (Benton et al. 2001). These lags in regulation also promote the possibility of cycles through delayed density-dependence (Turchin et al. 1999). Other causes of cycles are consumer-resource interactions such as predator-prey interactions (Lotka 1925; Volterra 1926), host-parasitoid, and host-pathogen interactions (Anderson and May 1981; Kendall et al. 1999), and periodic fluctuations in the environment with density-independent effects (Kendall et al. 1999).

population growth rate; Sibly and Hone 2002).

Sometimes, the disruptive effects of environmental stochasticity are of such magnitude that cannot be counteracted by endogenous mechanisms and thus a lack of population regulation can temporarily occur. Unregulated systems do not fluctuate around a long-term stationary probability distribution of population density (e.g., populations undergoing exponential growth/decline; Turchin 1995). An example of an extreme effect of environmental stochasticity is when a whole population is destroyed by means of catastrophic random events (Easterling et al. 2000; Singer and Thomas 1996). Extreme climatic events can promote such stochastic effects in population (and community) trajectory (Kreyling et al. 2011). Other examples of population deregulation are species' invasions and population density trends caused by anthropogenic changes in the environment. Identifying the relevant abiotic variables in population regulation is important to understand the mechanisms by which climate influences population ecology (Hallett et al. 2004).

B. LIFE-HISTORY TRADE-OFFS

One of the basic tenets of life-history theory states that different fitness-related traits are connected by constraining relationships derived from the allocation of limited resources (e.g., time, energy) between competing processes/functions within a single individual (Stearns 1992). Such linkages or *trade-offs* among traits are numerous and diverse, including those between current reproduction and survival, current reproduction and future reproduction, current reproduction and growth, and number and quality of offspring.

Perhaps because they are more straightforward, intrinsic trade-offs between life-history traits that share a finite resource pool occurring within the individual have received much more attention (Roff 1992; Stearns 1992). However, allocation decisions may also have ecological consequences (or "costs"), for example when a trade-off between reproduction and susceptibility to extrinsic threats such as predators or parasites exists (Sheldon and Verhulst 1996). In the same line, the most prominent trade-offs concern reproduction, and any change in a parent's strategy of resource allocation during reproduction is likely to have implications for their offspring (Stearns 1989). These intergenerational trade-offs can be a source of parent-offspring conflict and may have influenced the evolution of reproductive strategies and other associated life-history trade-offs, e.g., the trade-off between number and quality of offspring (Brown and Shine 2009; Dupoué et al. 2015; Kölliker and Richner 2001). Stearns (1992) addressed the former type of trade-off as physiological trade-offs and the latter as micro-evolutionary trade-offs, making a distinction between intrinsic or individual-level versus population-level trade-off constraints.

It is important to take into account that the apparent lack of a trade-off does not necessarily mean that it does not exist (Stearns 1989). Firstly, some trade-offs have been shown to be conditional and only become apparent when resources are limited, either in the environment or due to an individual's condition (e.g., under stressful conditions, Marden et al. 2003). Secondly, there may be variation in energy acquisition and allocation among individuals (Van Noordwijk and de Jong 1986), or genotype by environment interactions (Box 1.3; Reznick et al. 2000), preventing the observation of a trade-off.

Trade-offs commonly favor life-history plasticity and affect the evolution of most organisms in nature. It makes sense for traits with functional relationships to have integrated responses. When life-history traits have integrated, plastic responses,

Box 1.3 | Not so apparent trade-offs

Life-history trade-offs arise from genetic trade-offs (Reznick et al. 2000) when there is a genetic correlation between traits, which both positively affect fitness, but are negatively related to each other. These micro-evolutionary trade-offs (see main text) are expressed through physiological trade-offs and are defined by the population-level response to selection (Stearns 1992).

In Figure I, a trade-off between trait A and trait B shows different reaction norms in 3 alternative environments (e_1, e_2, e_3). The overall phenotypic correlation can be negative, but genetic correlations (bold lines) can be negative (left line) in some environments, positive (right line), or zero or non-significant (center, circle). Only when the correlation is negative can we perceive the trade-off, but genotype × environment interactions change the genetic correlations across environments (Stearns 1989).

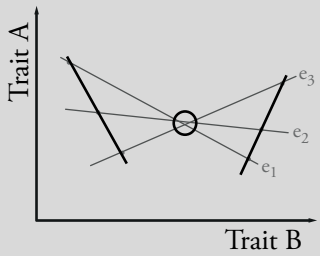


Figure I | G × E interaction. Adapted from Stearns (1989).

selection for compensation is likely, such that plastic changes in one trait that decrease fitness are compensated with plastic changes in a different trait that increase it (Stearns 1992). Integrated plastic responses can be explained by intrinsic trade-offs or genetic correlations among traits (i.e., different traits controlled by the same genes) that may be involved in more than one trade-off, producing pleiotropy (i.e., one gene influences multiple phenotypic traits). For example, one of the leading theories of senescence is based on antagonistic pleiotropic effects: Pleiotropic genes with beneficial early-life effects on survival or reproductive output also have deleterious effects on survival or reproduction later in life (Rose and Charlesworth 1980; Williams 1957). Ultimately, it is lifetime fitness that matters. Trade-offs can promote or constrain divergence (Cummings 2007; Haak et al. 2011) and adaptation (Colautti et al. 2010). Plasticity itself can be susceptible of short-term evolutionary change (Stearns 1992). However, in order to be evolutionarily relevant, plasticity must have a genetic basis (Reznick et al. 2000).

Life-history trade-offs—whether these take place within the lifetime of an individual or across generations—and plasticity underlie many delayed density-dependent effects with consequences for population dynamics (Beckerman et al. 2002). Trade-offs between current and future fitness, for example, such as early life reproductive expenditure versus lifetime survival, introduce lagged effects on population density (see

Box 1.2). More significantly, delayed life-history effects can give rise to *cohort effects* when all individuals in a cohort experience common environmental conditions that produce differences in their future performance compared to other cohorts (Beckerman et al. 2002). In structured populations, environmental conditions shared by any stage can lead to cohort effects (Albon et al. 1987). Through maternal effects, individual life-history responses can be transmitted between generations, potentially generating cohort effects on offspring (Benton et al. 2005; Benton et al. 2001).

Finally, environmental variability can directly influence trade-offs (or behaviors that affect trade-offs), which leads to delayed changes in individual survival or reproduction, or indirectly through the impact of the maternal environment on offspring. In such ways, current environmental effects are translated by a trade-off into a change in density, further resulting in a density-dependent effect at a later time (Beckerman et al. 2002).

Proximate causes of life-history trade-offs

In a general sense, the mechanisms underlying life-history trade-offs are still poorly studied. Most of the physiological processes related to growth, reproduction, and storage/allocation of resources are under the regulation of the endocrine system. Thus hormones may constitute an important component of animal life-history (Flatt and Heyland 2011). Hormones commonly mediate different physiological processes simultaneously, and in turn, a single process is affected by the action of multiple hormones, creating complex physiological networks that result in correlated patterns in phenotypic trait responses (Stearns 1992). This makes hormones (and endocrine regulation) an obvious candidate mechanism to mediate phenotypic correlations (Sinervo and Svensson 1998).

But what are the processes that create trade-offs? The traditional concept of trade-off (i.e., intrinsic trade-off) is based on the limited availability of critical resources that must be allocated into competing functions (see above, Van Noordwijk and de Jong 1986). Another possibility more recently described is that trade-offs are caused by signaling networks, independent of the allocation of critical resources to competing life-history functions (Leroi 2001). In trade-offs mediated by molecular signals, environmental or physiological cues are "sensed by the neurosensory apparatus, and integrated and processed into hormonal signals within endocrine cells. In target tissues, cognate receptors coordinate metabolism, growth, reproduction, homeostasis, and stress responses to ensure maximal reproductive success." (Flatt and Heyland

2011; Lessells 2008). In other words, the endocrine networks that regulate metabolism also respond to abiotic and social stressors that trigger a signaling cascade that operates through physiological and molecular response pathways with pleiotropic effects (i.e., multiple phenotypic expressions) on life-history traits (Box 1.4, Figure 1.3; Lancaster and Sinervo 2011; Schwartz and Bronikowski 2011; Sinervo and Svensson 1998). The opportunity for context-dependent modulation of the physiological pathways involved in a trade-off confers tremendous potential for plasticity of phenotypes along the trade-off continuum with adaptive value (Alonzo and Sinervo 2001; Dufty et al. 2002; Sinervo and Miles 2011). Both the social (e.g., crowding) and abiotic (e.g., weather) context could trigger a stress response that alters the expression of genetic trade-offs through multiple mechanisms (Figure 1.3; DeWitt et al. 1998; Sinervo et al. 2008; Snell-Rood et al. 2010). For example, it has been suggested that in social systems, epistasis (i.e., an interaction between genes that modifies their expression) between the genes present in one individual and those present in other social actors could alter the allocation of resources to competing life-history functions within interacting individuals, a process in turn mediated through pleiotropy. Consequently, life-history trade-offs could result from social interactions (Sinervo et al. 2008; Sinervo and Miles 2011), and social interactions promote polymorphism (i.e., alternative trait phenotypes) in life strategies (Lancaster and Sinervo 2011). In temporal and/or spatially variable conditions, gene interactions can maintain polymorphisms within populations (Sinervo et al. 2008).

The vast majority of research on the endocrine regulation of life-history trade-offs has been conducted on the effects of steroid hormones (Sinervo and Svensson 1998). Among them, glucocorticoids ("stress hormones") and androgens ("sex hormones") are the most common. Because glucocorticoids are the main products of the physiological response to environmental stressors (see Box 1.4), they are perfect candidates for the study of life-history plasticity in response to external cues. Environmental stressors importantly affect the hormonal regulation of behavior; they have been shown to alter reproduction (e.g., mating decisions, reproductive investment) and metabolic physiology and consequently stress hormones likely mediate important life-history trade-offs, e.g., between reproduction and longevity (Figure 1.3; Schwartz and Bronikowski 2011; Tokarz and Summers 2011).

It is worth noting that the physiological and cellular responses to environmental and metabolic stress differ between endothermic and ectothermic organisms. On the one hand, the ability to regulate their metabolic function through behavioral

Box 1.4 | The stress response in vertebrates

In response to a stress factor (e.g., dietary, predatory, temperature, agonistic social interactions) that disrupts homeostasis, vertebrates usually initiate a physiological stress response triggered by the activation of the hypothalamic–pituitary–adrenal (HPA) axis (Figure I), which is regulated by both the central and peripheral nervous systems. The initial release of the neurotrans-mitter noradrenaline by the sympathetic nervous system stimulates the synthesis and release of vasopressin and corticotropin-releasing hormone (CRH) at the hypothalamus. Both hormones stimulate the pituitary gland (hypophysis) to produce adrenocorticotropic hormone (ACTH), which in turn stimulates the adrenal glands' cortex to secrete glucocorticoids. Glucocorticoids are involved in a general process of diverting energy to immediate survival functions such as gluconeogenesis (synthesis of glucose), the mobilization of stored glucose (its release into circulating blood), and the reduction of the immune response (inflammation; Hickman et al. 2001). In many birds, reptiles, amphibians and some small mammals, corticosterone (CORT) is the main glucocorticoid released, whose concentration rises in the blood stream within few minutes (Tokarz and Summers 2011), while cortisol is released in fish, primates and other mammals.

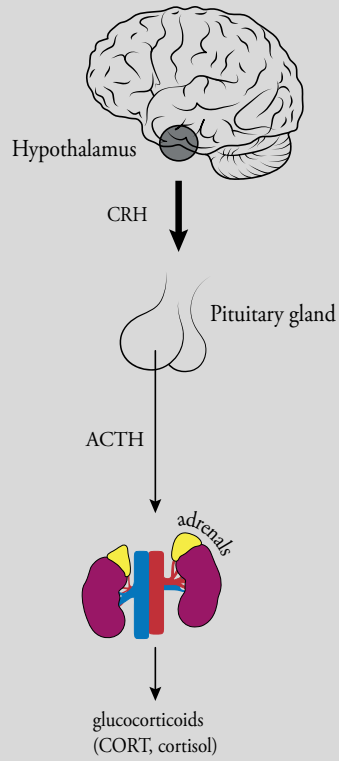


Figure I | The neuroendocrine pathway of the stress response in vertebrates (HPA axis), regulating hormones and products: Corticotropin-releasing hormone (CRH); adrenocorticotropic hormone (ACTH); corticosterone (CORT).

modulation of their body temperature has conferred ectotherms immense flexibility of lifestyles and the capacity to acclimate life-history traits to local spatial and temporal variation in resource availability (Shine 2005). On the other hand, inhabiting environments with stochastic variation of thermal or hydric conditions may represent an extra cost for ectothermic animals due to higher metabolic costs of acclimation (Kassahn et al. 2009). In any case, the molecular pathway of the stress response (e.g., HPA axis components) and its functionality is highly conserved across evolution, including invertebrate (e.g., honeybees) and vertebrate species (Box 1.4; Huising and Flik 2005; Westphal and Seasholtz 2006), emphasizing its key adaptive role.

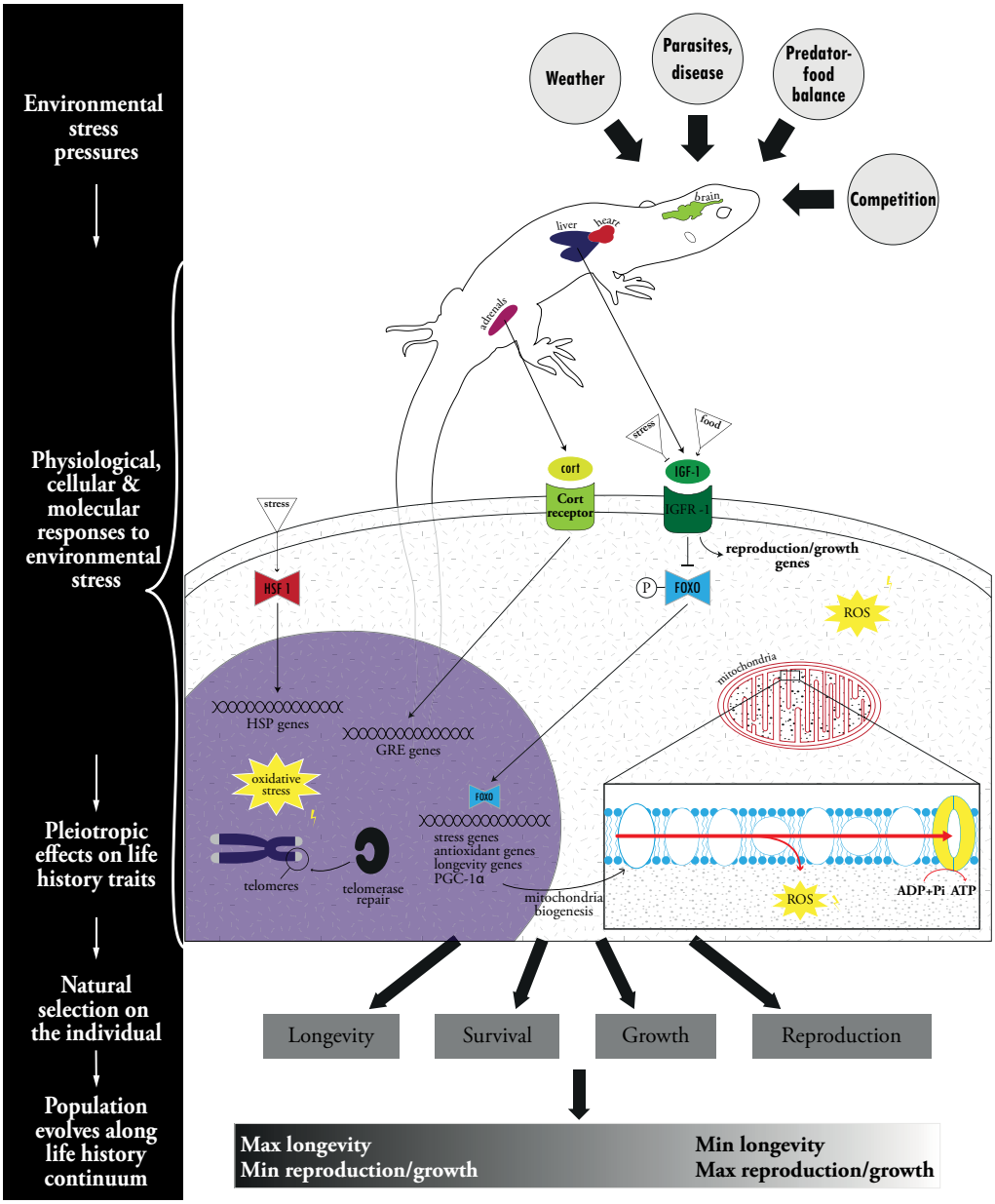


Figure 1.3 Plastic modulation of life-history traits through molecular/physiological pathways with pleiotropic effects involved in the trade-off between longevity and reproduction/growth. Cort effects (Box 1.4) result from transcription activation of genes with encoding glucocorticoid response elements (GRE). Cytoplasmic transcription factors (e.g., FOXO) are inhibited by the binding of IGF-1, eventually activating genes for growth/reproduction. In the absence of IGF-1 (e.g., under stress), FOXO enters the nucleus and activates genes for stress response/longevity. Metabolic pathways of energy (ATP) production release reactive oxygen species (ROS) that produce oxidative stress causing cellular (e.g., DNA) damage, which eventually decrease lifespan. Heat shock genes (HSP) up-regulate under heat stress, increasing growth rate (metabolic rate) and ROS production, thus mortality. Adapted from Schwartz and Bronikowski (2011).

On the adequacy of the common lizard as a model species and the experimental manipulation approach

Reptiles, lizards among them, are tremendously diverse in their life-history traits and show high environmental plasticity (Dunham and Miles 1985; Shine 2005), which *a priori* would suggest a high flexibility to adjust life-history traits to local environmental change. However, at least in Europe, species' assemblages of reptiles have been found to be relatively more distant from equilibrium with present-day climate than plants and breeding birds. As a result, reptile responses to climate change are harder to forecast accurately by current climatic models that precisely rely on the correlation between current distributions and climatic variables (Araújo and Pearson 2005; see also page 18). Furthermore, climatic change is expected to affect ectotherms such as reptiles particularly quickly, given their dependence on environmental abiotic conditions. The poor dispersal ability of many reptiles is also likely to contribute substantially to a slower response against local environmental alteration since this affects their capacity to shift their geographical distribution, which makes them extremely vulnerable to rapid climatic change (Araújo et al. 2006). However, a short-term shift of distribution in response to environmental change could be unnecessary if a species has sufficient innate phenotypic plasticity (Kerr and Kharouba 2007). Yet this may also increase the species' vulnerability over the long term if further *in situ* responses to change become constrained, hindering adaptation (e.g., because the limit of plasticity is reached), by reducing the opportunity for selection (Logan et al. 2014) or due to negative, delayed or correlative effects on local population dynamics. The overall reported decline of reptile species across the globe in recent decades (Araújo et al. 2006; Gibbons et al. 2000; Sinervo et al. 2010) justifies the current concern for their conservation (Böhm et al. 2013), emphasizes the lack of available data and studies on the possible causes of reptile population declines (Pacifici et al. 2015) and calls for a better understanding of the drivers of local dynamics and the traits that characterize their sensitivity and adaptive capacity.

The common lizard, *Zootoca vivipara* (Lichtenstein, 1823)(= *Lacerta vivipara*), is the only species of the genus *Zootoca*, subfamily Lacertinae (Squamata: Lacertidae)(Pyron et al. 2013) and the extant reptile with the widest geographical distribution. It mainly occupies the Temperate Zone in Eurasia, from Ireland and Galicia (Spain) in the west to Japan (Hokkaido island) and Russia (Sakhalin island) in the east, and from Scandinavia (within the Arctic Circle) in the north to northern Spain, northwestern

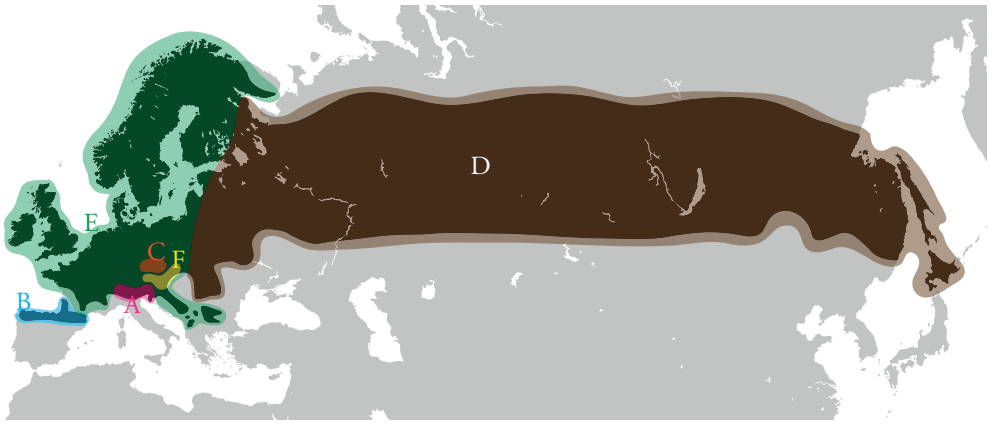


Figure 1.4 World distribution of *Z. vivipara* (in black), recognized lineages (in colors) and corresponding subspecies: A) eastern oviparous clade (*Z. v. carniolica*); B) western oviparous clade (*Z. v. louislantzi*); C) first central viviparous clade (*Z. v. vivipara* = *Z. v. pannonica*); D) eastern viviparous clade (*Z. v. sachalinensis*); E) western viviparous clade (*Z. v. vivipara* = *Z. v. pannonica*); F) second central viviparous clade (*Z. v. vivipara*). Based on Arribas (2009) and Surget-Groba et al. (2006).

Macedonia and southwestern Bulgaria in the south (Figure 1.4; Agasyan et al. 2010; Salvador 2014). Such an ample distribution is commonly attributed to the species' ecological plasticity and life-history variation (Adolph and Porter 1993; Lorenzon et al. 2001). *Z. vivipara* is one of the few reptiles that exhibit a bimodal reproductive system: some populations are viviparous (live-bearing) while others are oviparous (egg-laying). Viviparous forms presumably evolved under cold environments and allowed the species to colonize new areas of unfavorable climate (Heulin et al. 1999; Rodriguez-Diaz and Braña 2012; Surget-Groba et al. 2006; Tinkle and Gibbons 1977).

Within its distribution range, different clades have been identified based on mitochondrial DNA analyses, karyotype features and reproductive mode but so far recognized subspecies remain scarce (Arribas 2009; Surget-Groba et al. 2006; Surget-Groba et al. 2001; also see Cornetti et al. 2015, suggesting the separation of clades A and E in the Alps into two different species). In the Iberian Peninsula, phylogenetic analyses based on mitochondrial and nuclear DNA have revealed four main lineages corresponding to the French and Spanish sides of the Pyrenees, the Basque country and the Cantabro - Galician mountains, namely "Southern France" clade (French Pyrenees), "NE Spain" clade (Pyrenees), "north-central Spain" clade (Eastern Cantabrian Mountains and Basque Country), and "NW Spain" clade (Western Cantabrian Mountains; Milá et al. 2013). The subspecies *Z. vivipara louislantzi* Arribas 2009 was recently described for the Cantabro-Pyrenean populations (= western

oviparous clade (B, Figure 1.4; Arribas 2009). The populations established for the purposes of this thesis were composed of individuals exclusively originating from the Pyrenean clade ("NE Spain" clade sensu Milá et al. 2013).

Lifestyle, Ecology and Habitat

Z. vivipara is a diurnal, small lizard (adult snout-to-vent length, SVL: 45-70 mm) with ground-dwelling habits (House et al. 1980) that preys on small invertebrates, including Araneae and Homoptera (Avery 1966; Avery 1971; Heulin 1986). The existence of sexual dimorphism and distinct developmental stages during ontogeny are related to the ample variability of features among individuals within populations, whether morphological, ecological or phenological. The annual activity period extends from February-April to late September-October depending on sex, age and climatic conditions and hibernation takes place from then on until the next spring (Bauwens and Verheyen 1987; Roig et al. 2000). Adult males emerge prior to females and younger individuals (van Nuland and Strijbosch 1981) and mating occurs immediately after female emerge from hibernation (Bauwens and Verheyen 1985; Breedveld and Fitze 2015). Hibernation is necessary for vitellogenesis, thus the completion of female ovarian cycle, and reproduction (Gavaud 1983). Average life expectancy (of individuals that survived their first year) is 5 years (Avery 1975a), and female life expectancy is longer than the male's (Richard et al. 2005; Ronce et al. 1998). All individuals over two years are reproductively active, and some reproduce during their first year of life if a minimum body size is attained, because sexual maturity depends on body size rather than age (Bauwens 1999; Heulin 1985b).

During development, individuals can be classified in three distinct age classes (Figure 1.5): juvenile, subadult (yearling) and adult stage. Sexual dimorphism is less conspicuous in juveniles and at this stage sex can be determined by ventral scale count (Lecomte et al. 1992), a character that remains constant throughout the lizard's life (Bauwens and Verheyen 1987). From subadult stage onwards at least some secondary sexual traits are unambiguously recognizable (e.g., ventral coloration, femoral pores, thickness of the tail base, distinct body size; Figure 1.5) and used in sex identification.

The mating system is polygynandrous, and reproducing males have on average more partners than females (Laloi et al. 2004). Antagonistic competition among males and context-dependent female mate choice determine male mating success (Fitze et al. 2008; Fitze et al. 2005; Heulin 1988; San-Jose et al. 2014). Bigger, and in better condition males are typically more successful (Fitze et al. 2010; Heulin 1988) and tail

length and bite force also affect male reproductive success (Huyghe et al. 2013). Females can lay up to three clutches in one reproductive season (Roig et al. 2000) and clutch size is positively correlated with female body size (Avery 1975b; Pilorge et al. 1983). Trade-offs between the size and number of offspring (Bauwens 1999), current and future reproduction (Bleu et al. 2013; Le Galliard et al. 2008), early reproduction and late-life performance (senescence; Massot et al. 2011) and between reproductive investment and immune function (Meylan et al. 2013) have been reported. The species does not present parental care, juveniles are autonomous after birth/hatching, and

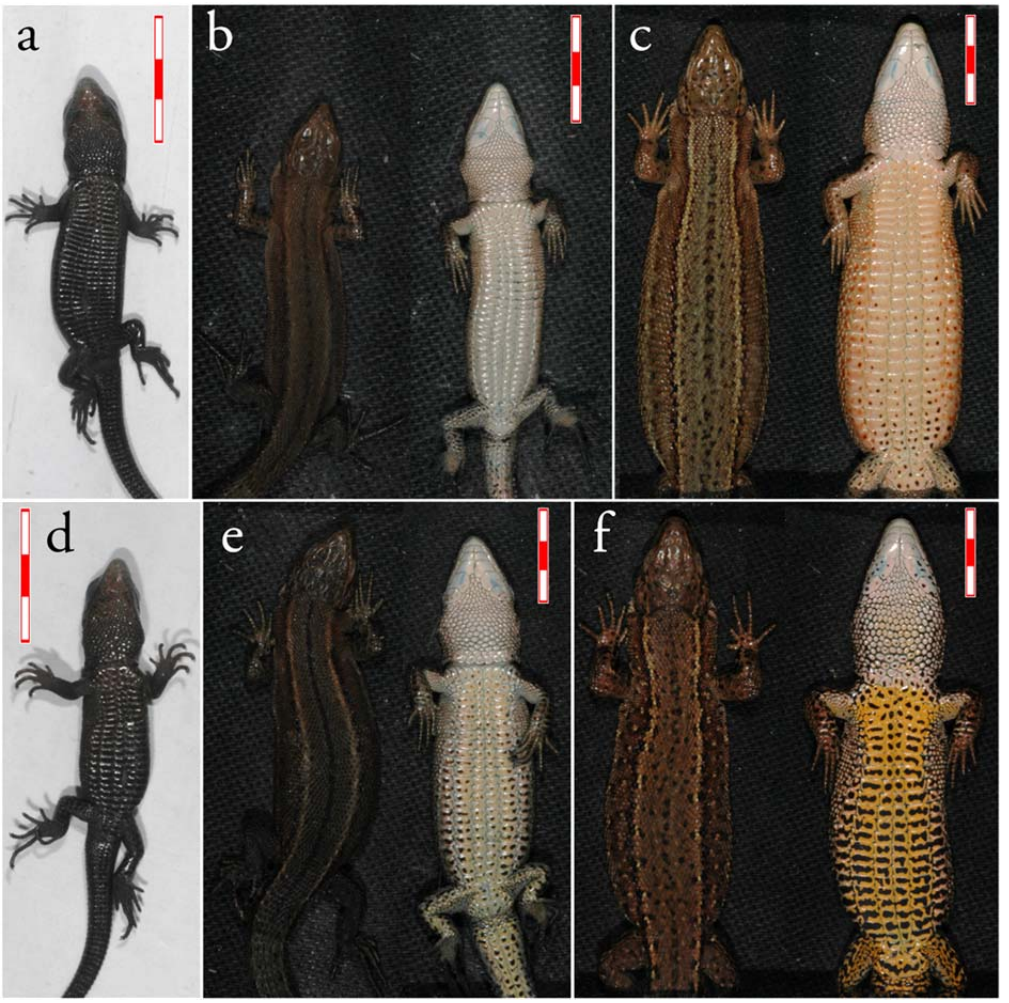


Figure 1.5 Female (above) and male (below) ontogenetic stages: (a, d) juvenile; (b, e) subadult; and (c, f) adult. Dorsal and ventral views (only ventral for juveniles) of six different individuals are shown. Sexual dimorphism is conspicuous from subadult stage onwards. Image scale is 1:1 in c and f.

only oviparous females search for specific oviposition sites (van Nuland and Strijbosch 1981). Incubation conditions like temperature influence incubation time and newborn morphology (Rodriguez-Diaz and Braña 2012; Rodríguez-Díaz et al. 2010).

Common lizards usually occupy humid soil habitats such as peatbogs and heathlands with bushy vegetation. They are abundant near watercourses in grasslands and shrublands surrounding forested areas with sufficient environmental humidity (Castroviejo et al. 1970; Grenot and Heulin 1990; Salvador 2014). In the Iberian Peninsula the species is confined to the Eurosiberian climatic region, well-characterized by a shorter duration of the dry season and much lower aridity (i.e., more precipitation and more days with rainfall throughout the year; Moreno et al. 1990), which suggests humidity is the most relevant abiotic environmental factor limiting its distribution (Ceirans 2007). In fact, *Z. vivipara* is highly vulnerable to hydric loss due to its elevated rate of evaporative water loss, through the skin and respiration (Grenot and Heulin 1990; Grenot et al. 1987). Furthermore, water constraints affect growth, activity patterns, reproduction and survival (Le Galliard et al. 2010; Lorenzon et al. 2001; Lorenzon et al. 1999; Marquis et al. 2008) relatively more than mean temperature conditions (Clusella-Trullas et al. 2011; Le Galliard et al. 2010).

Population dynamic

Common lizard populations are stage-structured with overlapping generations. Population density is generally highly variable (Grenot and Heulin 1990; Heulin 1985a; Pilorge 1981; Pilorge 1982; Pilorge 1987), and it is usually higher in humid habitats presumably due to the presence of more abundant trophic resources (Heulin 1985a; Heulin 1986). Female survival is negatively affected by density (Pilorge et al. 1987) and male-biased sex ratios (Le Galliard et al. 2005c). Adult sex ratio varies from one region to another, although the average found across European populations is female-biased (Heulin et al. 1997).

Population dynamic is vastly complex, affected by density-dependent factors (Massot et al. 1992) operating through, e.g., asymmetric inter-cohort competition for trophic resources, parasite incidence (Mugabo et al. 2015; Mugabo et al. 2013), or delayed effects of conditions experienced during early development (Massot and Aragon 2013; Mugabo et al. 2010). Other factors influencing population regulation are maternal effects and socially-acquired information about density on patterns of juvenile dispersal (Bestion et al. 2014; Cote et al. 2008; Massot and Clobert 1995; Meylan and Clobert 2004), and climatic conditions, which are associated with intra-

cohort variation (Le Galliard et al. 2010). In the Pyrenean oviparous clades, adult males exhibit a color polymorphism with six alternative morphs that behave like a single locus with 3 alleles (orange, *o*; yellow, *y*, and white, *w*; San-Jose et al. 2014; Sinervo et al. 2007). Morphs can be classified on the basis of the number of putative color alleles using two color scores (*o* score: 2 = *oo*; 1 = *yo*, *wo*; 0 = *yy*, *wy*, and *ww*; and *w* score: 2 = *ww*; 1 = *wy*, *wo*; 0 = *yy*, *yo*, and *oo*). The dominant morph frequency in the population cycles in agreement with rock-paper-scissors (RPS) dynamics (Sinervo et al. 2007) consisting of three intransitive morphs (≈ strategies), where each morph prevails over another and is defeated by a third. Rapid morph cycles have been suggested to be maintained by cumulative episodes of frequency-dependent selection imposed by female mate choice on male morphs and frequency-dependent selection on juvenile survival (San-Jose et al. 2014).

Experimental populations system

The experiments included in this thesis were carried out using an experimental system that allowed monitoring the demographic changes of closed populations of common lizards and manipulating specific environmental conditions under an otherwise standardized environment. The experimental populations system is located near the Pyrenean Institute of Ecology in Jaca (central Pyrenees, Huesca, Spain) at 820 m a.s.l. It consists of 16 semi-natural common lizard populations maintained in outdoor enclosures (10 x 10 m). Each enclosure is delimited by galvanized metal walls buried into the ground that reach 1 m high above the surface (Figure 1.6). A covering net prevents avian predation and the surrounding walls prevent both lizard migration and the intrusion of terrestrial predators. All enclosures consist of standardized habitat, containing vegetation, water ponds, rocks and logs providing lizards with sites for hiding or hibernating, and thermoregulation. Irrigation is controlled trough an automatic sprinkling system, vegetation is mechanically controlled with regularity, and food is naturally available (e.g., Araneae, Homoptera, Orthoptera, Coleoptera, Hymenoptera, larvae of Lepidoptera, Oligochaeta). The established common lizard populations conform to the age structure and density observed in natural populations. More information can be found in the methods section of the following chapters (chapters I and II).

The use of experimental systems such as this one, allows us to test hypotheses to confirm whether a putative agent of population regulation is causally linked to the dynamic of the species, or simply associated with it (Caughley 1994). Experiments

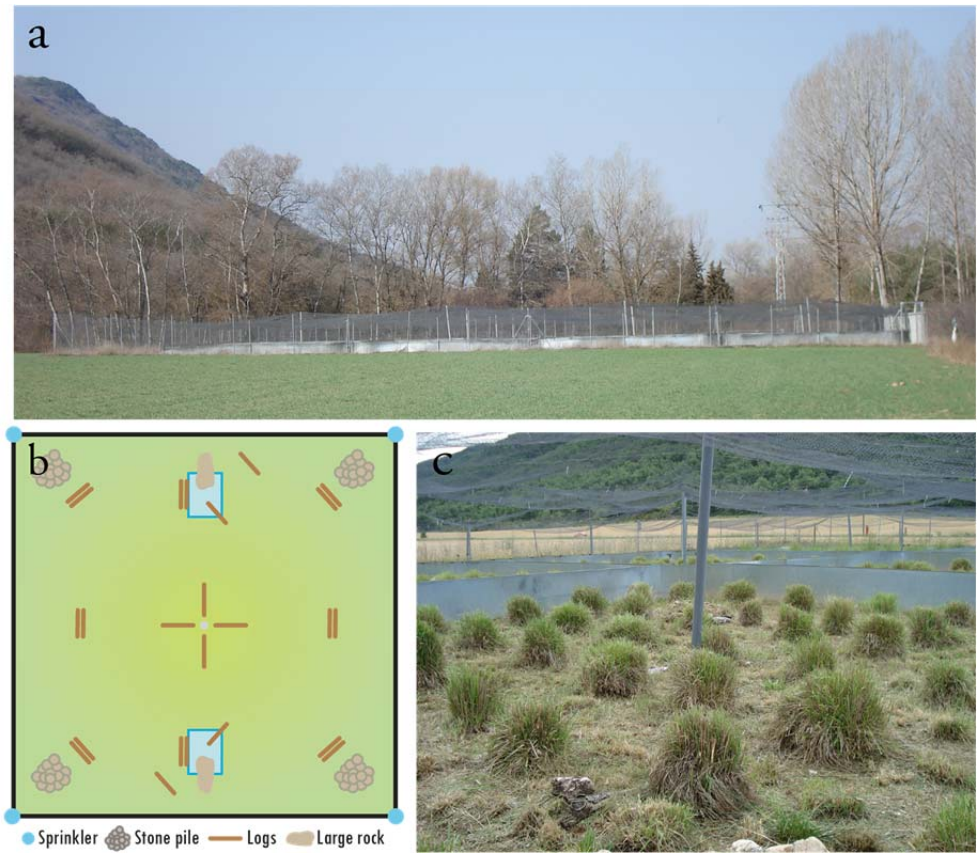


Figure 1.6 (a) Distant view of the complete experimental populations system in Jaca (Huesca, Spain); (b) diagram of an enclosure's set up and (c) actual appearance of an enclosure.

provide stronger inferences than field observations on the effects of environmental variables because they allow to control extrinsic factors (environmental variability) and remove confounding variables, contributing to the reduction of unexplained or biased trait variances (Sibly and Hone 2002) to reveal true causal effects. For this reason, causal hypotheses can only be tested with manipulative studies (i.e., experiments), exposing the biological mechanisms underlying population regulation (Turchin 1995) and providing an important link between modeling theory and field observation (Benton and Beckerman 2005). Based on these advantages, an experimental approach was considered appropriate for the purpose of this thesis project, namely: to assess relationships of causation between environmental (biotic and abiotic) conditions and individual life-history variation, in order to understand the mechanisms that determine population dynamics of *Z. vivipara*.

OBJECTIVES

The general objective of this thesis is to contribute reliable knowledge on the mechanisms underlying demographic processes of population regulation. This knowledge is fundamental to guide conservation efforts in the face of current and future climatic change (Dawson et al. 2011; Pacifici et al. 2015). Using an experimental approach, we investigate the effects of exogenous (i.e., climate) and endogenous factors on individual life-histories that in turn determine population dynamics (Benton and Beckerman 2005; Steiner et al. 2014). We use structured populations of *Z. vivipara* as a model system to reveal cause-effect responses to environmental change in an ectotherm species from a currently underrepresented and vulnerable taxon (reptiles).

The first part of this thesis (from chapters I to III) is concerned with the population-level dynamics of common lizards and the biological mechanisms behind them, with special interest on the role played by the abiotic environment and population structure. As it has been mentioned in the previous section, a determinant factor in the distribution and ecology of this species is habitat humidity, and thus it was chosen for experimental manipulation. Climate observations show that changes are occurring in the amount, intensity, frequency and type of precipitation (IPCC 2013). Therefore, three aspects of water availability/supply, which determine the level of habitat humidity, are investigated: total amount, stochasticity, and intensity.

In **chapter I** we examine the effects of habitat humidity (exogenous factor), in terms of amount, and population genetic characteristics (i.e., morph frequencies; endogenous factor) on life-history traits of different age classes. We address four principal questions to reveal the potential mechanism(s) involved in population regulation: 1) Do abiotic conditions (habitat humidity) affect life-histories of individuals? 2) Do abiotic conditions interact with the genetic characteristics during population regulation? 3) Are the effects of habitat humidity and/or genetic characteristics immediate or delayed (or both)? 4) How is inter-age class competition affected by these effects and what are the consequences at the population level?

In **chapter II** we investigate the effects of abiotic stochasticity, in terms of frequency and intensity of precipitation events, on life-history traits of different age classes. We study whether increased stochasticity would reduce population growth rate and increase the chance of population extinction as theory posits (Drake 2005; Saether and Engen 2004) and the effects that high intensity events (extreme events) may have at the

population level. We also investigate the mechanisms involved in the potential changes in population dynamics. In particular, we address the questions: 1) What are the effects of increased stochasticity on key life-history traits (individual growth, survival and reproduction)? 2) What are the effects of extreme events? 3) Do stochasticity and extreme events' effects interact? 4) How does this affect short- and long-term population dynamic?

In **chapter III** we explore whether and how habitat humidity and the adult morph frequency of the population affect frequency-dependent sexual selection, or more specifically, the patterns of male-morph competitiveness and thus the effects of exogenous and endogenous factors on female mate choice and/or male-male competition. We further discuss the consequences of such effects on male reproductive success for the maintenance of common lizards' polymorphism and the RPS dynamics of populations.

The second part of this thesis (**chapter IV**) focuses on individuals to explore, with a higher level of detail, one of the proximate mechanisms that might be operating in life-history variation at the organism level, which in turn could explain some of the changes observed at the population level. In **chapter IV** we test the effects of corticosterone (a glucocorticoid) in female mating behavior in the context of sexual conflict and its consequences for reproduction. Specifically: 1) Do females try to reduce the costs of mating during context-dependent mate choice? 2) Could hormones (such as corticosterone) be mediating these plastic responses?

Finally, I present a general discussion on the main findings of previous chapters and lay out the conclusions reached.

References

Adolph, S. C., and W. P. Porter. 1993. Temperature, activity, and lizard life-histories. American Naturalist 142:273-295.

Agasyan, A., A. Avci, B. Tuniyev, J. Crnobrnja Isailovic, P. Lymberakis, D. Andrén, C. Cogalniceanu et al. 2010. *Zootoca vivipara*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org.

Albon, S. D., T. H. Cluttonbrock, and F. E. Guinness. 1987. Early development and population-dynamics in red deer. II. Density-independent effects and cohort variation. Journal of Animal Ecology 56:69-81.

Alonzo, S. H., and B. Sinervo. 2001. Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard, *Uta stansburiana*. Behavioral Ecology and Sociobiology 49:176-186.

Allan, R. P., and B. J. Soden. 2008. Atmospheric warming and the amplification of precipitation extremes. Science 321:1481 - 1484.

Anderson, R. M., and R. M. May. 1981. The population dynamics of microparasites and their invertebrate hosts. Philosophical Transactions of the Royal Society B: Biological Sciences 291:451-524.

Araújo, M. B., and R. G. Pearson. 2005. Equilibrium of species' distributions with climate. Ecography 28:693-695.

Araújo, M. B., and C. Rahbek. 2006. How does climate change affect biodiversity? Science 313:1396-1397.

Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712–1728.

Araújo, M. B., R. J. Whittaker, R. J. Ladle, and M. Erhard. 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14:529-538.

Arnell, N. W. 1999. The effect of climate change on hydrological regimes in Europe: a continental perspective. Global Environmental Change 9:5 - 23.

Arribas, O. J. 2009. Morphological variability of the Cantabro-Pyrenean populations of *Zootoca vivipara* (Jacquin, 1787) with description of a new subspecies (Squamata: Sauria: Lacertidae). Herpetozoa 21:123-146.

Avery, R. A. 1966. Food and feeding habits of common lizard (*Lacerta vivipara*) in west of England. Journal of Zoology 149:115-&.

—. 1971. Estimates of food consumption by lizard *Lacerta vivipara* Jacquin. Journal of Animal Ecology 40:351-365.

—. 1975a. Age-structure and longevity of Common lizard (*Lacerta vivipara*) populations. Journal of Zoology 176:555-558.

—. 1975b. Clutch size and reproductive effort in the lizard *Lacerta vivipara* Jacquin. Oecologia 19:165-170.

Baker, A. C., C. J. Starger, T. R. McClanahan, and P. W. Glynn. 2004. Coral reefs: Corals' adaptive response to climate change. Nature 430:741-741.

Barnett, T. P., J. C. Adam, and D. P. Lettenmaier. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303 - 309.

Bauwens, D. 1999. Life-history variation in lacertid lizards. Natura Croatica 8:239-252.

Bauwens, D., and R. F. Verheyen. 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. Journal of Herpetology 19:353-364.

—. 1987. Variation of reproductive traits in a population of the lizard *Lacerta vivipara*. Holarctic Ecology 10:120-127.

Beckerman, A. P., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology & Evolution 17:263-269.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365-377.

Benton, T. G., and A. P. Beckerman. 2005. Population dynamics in a noisy world: Lessons from a mite experimental system, Pages 143-181 Advances in Ecological Research, Academic Press.

Benton, T. G., S. J. Plaistow, A. P. Beckerman, C. T. Lapsley, and S. Littlejohns. 2005. Changes in maternal investment in eggs can affect population dynamics. Proceedings of the Royal Society B: Biological Sciences 272:1351-1356.

Benton, T. G., E. Ranta, V. Kaitala, and A. P. Beckerman. 2001. Maternal effects and the stability of population dynamics in noisy environments. Journal of Animal Ecology 70:590-599.

Bestion, E., A. Teyssier, F. Aubret, J. Clobert, and J. Cote. 2014. Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. Proceedings of the Royal Society B: Biological Sciences 281.

Bleu, J., J.-F. Le Galliard, P. S. Fitze, S. Meylan, J. Clobert, and M. Massot. 2013. Reproductive allocation strategies: a long-term study on proximate factors and temporal adjustments in a viviparous lizard. Oecologia 171:141-151.

Blums, P., A. Mednis, I. Bauga, J. D. Nichols, and J. E. Hines. 1996. Age-specific survival and philopatry in three species of European ducks: A long-term study. Condor 98:61-74.

Böhm, M., B. Collen, J. E. M. Baillie, P. Bowles, J. Chanson, N. Cox, G. Hammerson et al. 2013. The conservation status of the world's reptiles. Biological Conservation 157:372-385.

Bonduriansky, R., and C. E. Brassil. 2002. Rapid and costly ageing in wild male flies. Nature 420:377-377.

Breedveld, M. C., and P. S. Fitze. 2015. A matter of time: delayed mate encounter postpones mating window initiation and reduces the strength of female choosiness. Behavioral Ecology and Sociobiology 69:533-541.

Broussard, D. R., T. S. Risch, F. S. Dobson, and J. O. Murie. 2003. Senescence and age-related reproduction of female Columbian ground squirrels. Journal of Animal Ecology 72:212-219.

Brown, G. P., and R. Shine. 2009. Beyond size–number trade-offs: clutch size as a maternal effect. Philosophical Transactions of the Royal Society B: Biological Sciences 364:1097-1106.

Cappuccino, N., and P. W. Price. 1995. Population dynamics: New approaches and synthesis, Elsevier Science.

Castroviejo, J., S. Castroviejo, and A. Salvador. 1970. Algunos datos sobre la distribución de la lagartija de turbera, *Lacerta vivipara*, en España. Boletín Real Sociedad Española Historia Natural 68:135-145.

Caswell, H. 2001, Matrix population models: construction, analysis, and interpretation. Second Edition. Sunderland, MA, Sinauer Associates, Inc.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.

Ceirans, A. 2007. Microhabitat characteristics for reptiles *Lacerta agilis*, *Zootoca vivipara*, *Anguis fragilis*, *Natrix natrix*, and *Vipera berus* in Latvia. Russian Journal of Herpetology 14:172-176.

Clusella-Trullas, S., T. M. Blackburn, and S. L. Chown. 2011. Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. American Naturalist 177:738-751.

Clutton-Brock, T. H., and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1285-1298.

Cornetti, L., G. F. Ficetola, S. Hoban, and C. Vernesi. 2015. Genetic and ecological data reveal species boundaries between viviparous and oviparous lizard lineages. Heredity 115:517-526.

Cote, J., S. Boudsocq, and J. Clobert. 2008. Density, social information, and space use in the common lizard (*Lacerta vivipara*). Behavioral Ecology 19:163-168.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley et al. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528-1531.

Coulson, T., and H. C. J. Godfray. 2007. Single-species dynamics, Pages 257 *in* R. M. May, and A. R. McLean, eds. Theoretical Ecology: Principles and Applications. UK, Oxford University Press.

Chapman, J. L., and J. Reiss. 1998, Ecology: Principles and applications, Cambridge University Press.

Dai, A. 2011. Drought under global warming: a review. Wiley Interdisciplinary Reviews: Climate Change 2:45-65.

Darwin, C. 1859, On the origin of species by means of natural selection. London, John Murray.

—. 1872, The origin of species. London, John Murray.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond Predictions: Biodiversity conservation in a changing climate. Science 332:53-58.

De Roos, A. M., and L. Persson. 2003. Competition in size-structured populations: mechanisms inducing cohort formation and population cycles. Theoretical Population Biology 63:1-16.

De Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473-487.

DeWitt, T. J., and S. M. Scheiner. 2004, Phenotypic plasticity: Functional and conceptual approaches. New York, Oxford University Press.

DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution 13:77-81.

Drake, J. M. 2005. Population effects of increased climate variation. Proceedings of the Royal Society B: Biological Sciences 272:1823–1827.

Dublin, L. I., and A. J. Lotka. 1925. On the true rate of natural increase: As exemplified by the population of the United States, 1920. Journal of the American Statistical Association 20:305-339.

Dufty, A. M., J. Clobert, and A. P. Møller. 2002. Hormones, developmental plasticity and adaptation. Trends in Ecology & Evolution 17:190-196.

Dunham, A. E., and D. B. Miles. 1985. Patterns of covariation in life-history traits of Squamate reptiles: The effects of size and phylogeny reconsidered. American Naturalist 126:231-257.

Dupoué, A., F. Brischoux, F. Angelier, D. F. DeNardo, C. D. Wright, and O. Lourdais. 2015. Intergenerational trade-off for water may induce a mother–offspring conflict in favour of embryos in a viviparous snake. Functional Ecology 29:414-422.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: Observations, modeling, and impacts. Science 289:2068-2074.

Fitze, P. S., J. Cote, and J. Clobert. 2010. Mating order-dependent female mate choice in the poligynandrous common lizard *Lacerta vivipara*. Oecologia 162:331-341.

Fitze, P. S., J. Cote, J. P. Martínez-Rica, and J. Clobert. 2008. Determinants of male fitness: disentangling intra- and inter-sexual selection. Journal of Evolutionary Biology 21:246-255.

Fitze, P. S., J.-F. Le Galliard, P. Federici, M. Richard, and J. Clobert. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. Evolution 59:2451-2459.

Flatt, T., and A. Heyland. 2011. Mechanisms of life history evolution: The genetics and physiology of life history traits and trade-offs, Oxford University Press.

Foden, W. B., S. H. M. Butchart, S. N. Stuart, J.-C. Vié, H. R. Akçakaya, A. Angulo, L. M. DeVantier et al. 2013. Identifying the world's most climate change vulnerable

species: A systematic trait-based assessment of all birds, amphibians and corals. PLoS ONE 8:e65427.

Forchhammer, M. C., T. H. Clutton-Brock, J. Lindstrom, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70:721-729.

Gavaud, J. 1983. Obligatory hibernation for completion of vitellogenesis in the lizard *Lacerta vivipara* J. Journal of Experimental Zoology 225:397-405.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene et al. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:653-666.

Gregory, J. M., J. F. B. Mitchell, and A. J. Brady. 1997. Summer drought in northern midlatitudes in a time-dependent CO_2 climate experiment. Journal of Climate 10:662-686.

Grenot, C., and B. Heulin. 1990. Sur la plasticité ecophysiologique du lézard vivipare, *Lacerta vivipara* (*Reptilia, Lacertidae*). Bulletin de la Societe Herpetologique de France 54:1-22.

Grenot, C., B. Heulin, T. Pilorge, M. Khodadoost, A. Ortega, and Y. P. Mou. 1987. Water budget in some populations of the European common lizard, *Lacerta vivipara* Jacquin. Functional Ecology 1:131-138.

Groisman, P. Y., T. R. Karl, D. R. Easterling, R. W. Knight, P. F. Jamason, K. J. Hennessy, R. Suppiah et al. 1999. Changes in the probability of heavy precipitation: Important indicators of climatic change. Climatic Change 42:243-283.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993-1009.

Gurney, W. S. C., and R. M. Nisbet. 1985. Fluctuation periodicity, generation separation, and the expression of larval competition. Theoretical Population Biology 28:150-180.

Gurney, W. S. C., R. M. Nisbet, and J. H. Lawton. 1983. The systematic formulation of tractable single-species population models incorporating age structure. Journal of Animal Ecology 52:479-495.

Haldane, J. B. S. 1924. A mathematical theory of natural and artificial selection. Transactions of the Cambridge Philosophical Society 23:19-41.

Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and B. T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71-75.

Hayward, A. D., A. J. Wilson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2013. Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. Functional Ecology 27:184-195.

Heulin, B. 1985a. Densité et organisation spatiale des populations du lézard vivipare *Lacerta vivipara* (Jacquin, 1787) dans les landes de la région de Paimpont. Bulletin d'Ecologie 16:177-186.

—. 1985b. Maturité sexuelle et âge à la première reproduction dans une population de plaine de *Lacerta vivipara*. Canadian Journal of Zoology 63:1773-1777.

—. 1986. Estival diet and use of trophic resources in three populations of *Lacerta vivipara*. Acta Oecologica-Oecologia Generalis 7:135-150.

—. 1988. Observations sur l'organisation de la reproduction et sur les comportements sexuels et agonistiques chez *Lacerta vivipara*. Vie Milieu 38.

Heulin, B., K. Osenegg-Leconte, and D. Michel. 1997. Demography of a bimodal reproductive species of lizard (*Lacerta vivipara*): Survival and density characteristics of oviparous populations. Herpetologica 53:432-444.

Heulin, B., Y. Surget-Groba, A. Guiller, C. P. Guillaume, and J. Deunff. 1999. Comparisons of mitochondrial DNA (mtDNA) sequences (16S rRNA gene) between oviparous and viviparous strains of *Lacerta vivipara*: a preliminary study. Molecular Ecology 8:1627-1631.

Hickman, C. P., L. S. Roberts, and A. Larson. 2001, Integrated principles of zoology, McGraw-Hill.

House, S. M., P. J. Taylor, and I. F. Spellerberg. 1980. Patterns of daily behaviour in two lizard species *Lacerta agilis* L. and *Lacerta vivipara* Jacquin. Oecologia 44:396-402.

Huising, M. O., and G. Flik. 2005. The remarkable conservation of corticotropin-releasing hormone (CRH)-binding protein in the honeybee (*Apis mellifera*) dates the CRH system to a common ancestor of insects and vertebrates. Endocrinology 146:2165-2170.

Huyghe, K., L. M. San-Jose, M. Peñalver Alcázar, and P. S. Fitze. 2013. An ecomorphological analysis of the determinants of mating success. Biological Journal of the Linnean Society.

IPCC. 2013. Summary for policymakers *in* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels et al., eds. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, NY, USA., Cambridge University Press.

—. 2014b. Summary for policymakers *in* C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee et al., eds. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

Jiguet, F., A.-S. Gadot, R. Julliard, S. E. Newson, and D. Couvet. 2007. Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biology 13:1672-1684.

Jovani, R., and J. L. Tella. 2004. Age-related environmental sensitivity and weather mediated nestling mortality in white storks *Ciconia ciconia*. Ecography 27:611-618.

Kassahn, K. S., R. H. Crozier, H. O. Portner, and M. J. Caley. 2009. Animal performance and stress: responses and tolerance limits at different levels of biological organisation. Biological Reviews 84:277-292.

Keenan, T., J. Maria Serra, F. Lloret, M. Ninyerola, and S. Sabate. 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO2 matters! Global Change Biology 17:565-579.

Kendall, B. E., C. J. Briggs, W. W. Murdoch, P. Turchin, S. P. Ellner, E. McCauley, R. M. Nisbet et al. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. Ecology 80:1789-1805.

Kendall, B. E., J. Prendergast, and O. N. Bjørnstad. 1998. The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. Ecology Letters 1:160-164.

Kerr, J. T., and H. M. Kharouba. 2007. Climate change and conservation biology, Pages 257 *in* R. M. May, and A. R. McLean, eds. Theoretical Ecology: Principles and Applications. UK, Oxford University Press.

Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper et al. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202 - 2205.

Kölliker, M., and H. Richner. 2001. Parent–offspring conflict and the genetics of offspring solicitation and parental response. Animal Behaviour 62:395-407.

Kreyling, J., A. Jentsch, and C. Beierkuhnlein. 2011. Stochastic trajectories of succession initiated by extreme climatic events. Ecology Letters 14:758-764.

Laloi, D., M. Richard, J. Lecomte, M. Massot, and J. Clobert. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellite markers. Molecular Ecology 13:719-723.

Lancaster, L. T., and B. Sinervo. 2011. Epistatic social and endocrine networks and the evolution of life history trade-offs and plasticity, Pages 329-348 *in* T. Flatt, and A. Heyland, eds. Mechanisms of life history evolution: The genetics and physiology of life history traits and trade-offs, Oxford University Press.

Lande, R. 1982. A quantitative genetic theory of life-history evolution. Ecology 63:607-615.

Le Galliard, J.-F., J. Cote, and P. S. Fitze. 2008. Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. Ecology 89:56-64.

Le Galliard, J.-F., P. S. Fitze, R. Ferrière, and J. Clobert. 2005c. Sex ratio bias, male aggression, and population collapse in lizards. Proceedings of the National Academy of Sciences of the United States of America 102:18231–18236.

Le Galliard, J.-F., O. Marquis, and M. Massot. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. Journal of Animal Ecology 79:1296-1307.

Leadley, P., H. M. Pereira, R. Alkemade, J. F. Fernandez-Manjarrés, V. Proença, J. P. W. Scharlemann, and M. J. Walpole. 2010. Biodiversity Scenarios: Projections of 21st century change in biodiversity and associated ecosystem services, Pages 132, Technical Series no. 50. Montreal, Secretariat of the Convention on Biological Diversity.

Lecomte, J., J. Clobert, and M. Massot. 1992. Sex identification in juveniles of *Lacerta vivipara*. Amphibia-Reptilia 13:21-25.

Leroi, A. M. 2001. Molecular signals versus the *Loi de Balancement*. Trends in Ecology & Evolution 16:24-29.

Lessells, C. M. 2008. Neuroendocrine control of life histories: what do we need to know to understand the evolution of phenotypic plasticity? Philosophical Transactions of the Royal Society B: Biological Sciences 363:1589-1598.

Lincoln, R. J., G. A. Boxshall, and P. F. Clark. 1998, A dictionary of ecology, evolution and systematics, Cambridge University Press.

Logan, M. L., R. M. Cox, and R. Calsbeek. 2014. Natural selection on thermal performance in a novel thermal environment. Proceedings of the National Academy of Sciences of the United States of America 111:14165-14169.

Lorenzon, P., J. Clobert, and M. Massot. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. Evolution 55:392-404.

Lorenzon, P., J. Clobert, A. Oppliger, and H. John-Alder. 1999. Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). Oecologia 118:423-430.

Lotka, A. J. 1925, Elements of physical biology: Elements of Physical Biology., Williams & Wilkins, Baltimore.

Marden, J. H., B. Rogina, K. L. Montooth, and S. L. Helfand. 2003. Conditional tradeoffs between aging and organismal performance of *Indy* long-lived mutant flies. Proceedings of the National Academy of Sciences of the United States of America 100:3369-3373.

Marquis, O., M. Massot, and J.-F. Le Galliard. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. Ecology 89:2575-2583.

Massot, M., and P. Aragon. 2013. Phenotypic resonance from a single meal in an insectivorous lizard. Current Biology 23:1320-1323.

Massot, M., and J. Clobert. 1995. Influence of maternal food availability on offspring dispersal. Behavioral Ecology and Sociobiology 37:413-418.

Massot, M., J. Clobert, L. Montes-Poloni, C. Haussy, J. Cubo, and S. Meylan. 2011. An integrative study of ageing in a wild population of common lizards. Functional Ecology 25:848-858.

Massot, M., J. Clobert, T. Pilorge, J. Lecomte, and R. Barbault. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. Ecology 73:1742-1756.

May, R. C. 1974. Larval mortality in marine fishes and the critical period concept, Pages 3-19 *in* J. S. Blaxter, ed. The early life history of fish, Springer Berlin Heidelberg.

Mayr, E. 1998, This is biology: The science of the living world, Harvard University Press.

McMahon, S. M., S. P. Harrison, W. S. Armbruster, P. J. Bartlein, C. M. Beale, M. E. Edwards, J. Kattge et al. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. Trends in Ecology & Evolution 26:249-259.

Mearns, L. O., C. Rosenzweig, and R. Goldberg. 1997. Mean and variance change in climate scenarios: Methods, agricultural applications, and measures of uncertainty. Climatic Change 35:367-396.

Meylan, S., and J. Clobert. 2004. Maternal effects on offspring locomotion: Influence of density and corticosterone elevation in the lizard *Lacerta vivipara*. Physiological and Biochemical Zoology 77:450-458.

Meylan, S., M. Richard, S. Bauer, C. Haussy, and D. Miles. 2013. Costs of mounting an immune response during pregnancy in a lizard. Physiological and Biochemical Zoology 86:127-136.

Milá, B., Y. Surget-Groba, B. Heulin, A. Gosa, and P. S. Fitze. 2013. Multilocus phylogeography of the common lizard *Zootoca vivipara* at the Ibero-Pyrenean suture zone reveals lowland barriers and high-elevation introgression. BMC Evolutionary Biology 13:192.

Miles, D. B., and A. E. Dunham. 1992. Comparative analyses of phylogenetic effects in the life-history patterns of Iguanid reptiles. American Naturalist 139:848-869.

Miller, D. A. W., F. J. Janzen, G. M. Fellers, P. M. Kleeman, and A. M. Bronikowski. 2014. Biodemography of ectothermic tetrapods provides insights into the evolution and plasticity of mortality patterns. Comparative Biodemography: Sociality, Hierarchy, Health. Washington DC, The National Academies Press.

Moreno, J. M., F. D. Pineda, and S. Rivas-Martinez. 1990. Climate and vegetation at the Eurosiberian-Mediterranean boundary in the Iberian Peninsula. Journal of Vegetation Science 1:233-244.

Mugabo, M., O. Marquis, S. Perret, and J.-F. Le Galliard. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. Journal of Evolutionary Biology 23:1886 - 1898.

Mugabo, M., S. Perret, B. Decenciere, S. Meylan, and J.-F. Le Galliard. 2015. Density-dependent immunity and parasitism risk in experimental populations of lizards naturally infested by ixodid ticks. Ecology 96:450-460.

Mugabo, M., S. Perret, S. Legendre, and J.-F. Le Galliard. 2013. Density-dependent life history and the dynamics of small populations. Journal of Animal Ecology 82:1227-1239.

Nicotra, A. B., E. A. Beever, A. L. Robertson, G. E. Hofmann, and J. O'Leary. 2015. Assessing the components of adaptive capacity to improve conservation and management efforts under global change. Conservation Biology 29:1268-1278.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Australian Journal of Zoology 2:9-65.

Nussey, D. H., H. Froy, J.-F. Lemaitre, J.-M. Gaillard, and S. N. Austad. 2013. Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. Ageing Research Reviews 12:214-225.

Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R. Scheffers et al. 2015. Assessing species vulnerability to climate change. Nature Climate Change 5:215-224.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change, Pages 637-669 Annual Review of Ecology Evolution and Systematics.

Parmesan, C., T. L. Root, and M. R. Willig. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81:443-450.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Pfaff, T., A. Brechtel, B. Drossel, and C. Guill. 2014. Single generation cycles and delayed feedback cycles are not separate phenomena. Theoretical Population Biology 98:38-47.

Pigliucci, M. 2005. Evolution of phenotypic plasticity: where are we going now? Trends in Ecology & Evolution 20:481-486.

Pilorge, T. 1981. Structure et dynarnique d'une population du lézard vivipare. Signification adaptive de la viviparité chez les lézards. Bulletin de la Societé Herpetologique de France 18:29-31.

Pilorge, T. 1982. Stratégie adaptative d'une population de montagne de *Lacerta vivipara*. Oikos 39:206-212.

—. 1987. Density size, structure, and reproductive characteristics of 3 populations of *Lacerta vivipara* (Sauria, Lacertidae). Herpetologica 43:345-356.

Pilorge, T., J. Clobert, M. Massot, J. J. van Gelder, H. Strijbosch, and P. J. M. Bergers. 1987. Life history variations according to sex and age in *Lacerta vivipara*, Pages 311-315 Proceedings of the 4th Ordinary General Meeting of the Societas Europaea Herpetologica., Societas Europaea Herpetologica, Faculty of Sciences, Nijmegen.

Pilorge, T., F. Xavier, and R. Barbault. 1983. Variations in litter size and reproductive effort within and between some populations of *Lacerta vivipara*. Ecography 6:381-382.

Primack, R. B. 2004, A primer of conservation biology. Sunderland, MA, Sinauer Associates, Inc.

Pyron, R., F. Burbrink, and J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13:93.

Reed, T. E., L. E. Kruuk, S. Wanless, M. Frederiksen, E. J. Cunningham, and M. P. Harris. 2008. Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. American Naturalist 171:E89-E101.

Reznick, D., L. Nunney, and A. Tessier. 2000. Big houses, big cars, superfleas and the costs of reproduction. Trends in Ecology & Evolution 15:421-425.

Richard, M., J. Lecomte, M. de Fraipont, and J. Clobert. 2005. Age-specific mating strategies and reproductive senescence. Molecular Ecology 14:3147-3155.

Rodriguez-Diaz, T., and F. Braña. 2012. Altitudinal variation in egg retention and rates of embryonic development in oviparous *Zootoca vivipara* fits predictions from the cold-climate model on the evolution of viviparity. Journal of Evolutionary Biology 25:1877-1887.

Rodríguez-Díaz, T., F. Gonzalez, X. Ji, and F. Braña. 2010. Effects of incubation temperature on hatchling phenotypes in an oviparous lizard with prolonged egg retention: Are the two main hypotheses on the evolution of viviparity compatible? Zoology 113:33-38.

Roff, D. A. 1992, Evolution of life histories: Theory and analysis, Springer.

Roig, J. M., M. A. Carretero, and G. A. Llorente. 2000. Reproductive cycle in a Pyrenean oviparous population of the common lizard (*Zootoca vivipara*). Netherlands Journal of Zoology 50:15-27.

Ronce, O., J. Clobert, and M. Massot. 1998. Natal dispersal and senescence. Proceedings of the National Academy of Sciences of the United States of America 95:600-605.

Rose, M., and B. Charlesworth. 1980. A test of evolutionary theories of senescence. Nature 287:141-142.

Rudolf, V. H. W., and N. L. Rasmussen. 2013. Population structure determines functional differences among species and ecosystem processes. Nature Communications 4.

Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology & Evolution 12:143-149.

Saether, B. E., and S. Engen. 2004. Stochastic population theory faces reality in the laboratory. Trends in Ecology & Evolution 19:351-353.

Sala, O. E., F. Stuart Chapin , III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo et al. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Salvador, A. 2014. *Zootoca vivipara* (Lichtenstein 1823), Pages 640-651 *in* A. Salvador, ed. Fauna Ibérica. Vol. 10: Reptiles (2ª ed. rev. y aum.). Madrid, Consejo Superior de Investigaciones Científicas.

San-Jose, L. M., M. Peñalver-Alcázar, B. Milá, V. Gonzalez-Jimena, and P. S. Fitze. 2014. Cumulative frequency-dependent selective episodes allow for rapid morph cycles and rock-paper-scissors dynamics in species with overlapping generations. Proceedings of the Royal Society B: Biological Sciences 281:20140976.

Sclater, P. L. 1858. On the general geographical distribution of the members of the class Aves. Journal of the Proceedings of the Linnean Society of London. Zoology 2:130-136.

Schlichting, C. D., and H. Smith. 2002. Phenotypic plasticity: Linking molecular mechanisms with evolutionary outcomes. Evolutionary Ecology 16:189-211.

Schwartz, T. S., and A. M. Bronikowski. 2011. Molecular stress pathways and the evolution of life histories in reptiles, Pages 193-209 *in* T. Flatt, and A. Heyland, eds. Mechanisms of life history evolution: The genetics and physiology of life history traits and trade-offs, Oxford University Press.

Sheldon, B. C., and S. Verhulst. 1996. Ecological immunology: Costly parasite defences and trade-offs in evolutionary ecology. Trends in Ecology & Evolution 11:317-321.

Shine, R. 2005. Life-history evolution in reptiles, Pages 23-46 Annual Review of Ecology Evolution and Systematics. Annual Review of Ecology Evolution and Systematics. Palo Alto, Annual Reviews.

Shuster, S. M., and M. J. Wade. 2003, Mating systems and strategies. Princeton, NJ., Princeton University Press.

Sibly, R. M., and J. Hone. 2002. Population growth rate and its determinants: an overview. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1153-1170.

Sinclair, S. J., M. D. White, and G. R. Newell. 2010. How useful are species distribution models for managing biodiversity under future climates? Ecology and Society 15:8.

Sinervo, B., J. Clobert, D. B. Miles, A. McAdam, and L. T. Lancaster. 2008. The role of pleiotropy vs signaller-receiver gene epistasis in life history trade-offs: dissecting the genomic architecture of organismal design in social systems. Heredity 101:197-211.

Sinervo, B., B. Heulin, Y. Surget-Groba, J. Clobert, D. B. Miles, A. Corl, A. Chaine et al. 2007. Models of density-dependent genic selection and a new rock-paper-scissors social system. American Naturalist 170:663–680.

Sinervo, B., F. Méndez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. V.-S. Cruz, R. Lara-Resendiz et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894-899.

Sinervo, B., and D. B. Miles. 2011. Hormones and behavior of reptiles, Pages 215-246 *in* D. O. Norris, and K. H. Lopez, eds. Hormones and Reproduction of Vertebrates. London, Academic Press.

Sinervo, B., and E. Svensson. 1998. Mechanistic and selective causes of life history trade-offs and plasticity. Oikos 83:432-442.

Singer, M. C., and C. D. Thomas. 1996. Evolutionary responses of a butterfly metapopulation to human- and climate-caused environmental variation. American Naturalist 148:S9-S39.

Slatkin, M. 1974. Hedging one's evolutionary bets. Nature 250:704-705.

Snell-Rood, E. C., J. D. Van Dyken, T. Cruickshank, M. J. Wade, and A. P. Moczek. 2010. Toward a population genetic framework of developmental evolution: The costs, limits, and consequences of phenotypic plasticity. Bioessays 32:71-81.

Soulé, M. E. 1985. What is conservation biology? Bioscience 35:727-734.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional Ecology 3:259-268.

—. 1992, The evolution of life histories. Oxford, UK, Oxford University Press.

Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. Evolution 40:893-913.

Steiner, U. K., S. Tuljapurkar, and T. Coulson. 2014. Generation time, net reproductive rate, and growth in stage-age-structured populations. American Naturalist 183:771-783.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292-1296.

Sun, Y., S. Solomon, A. Dai, and R. W. Portmann. 2007. How often will it rain? Journal of Climate 20:4801-4818.

Surget-Groba, Y., B. Heulin, C.-P. Guillaume, M. Puky, D. Semenov, V. Orlova, L. Kupriyanova et al. 2006. Multiple origins of viviparity, or reversal from viviparity to oviparity? The European common lizard (*Zootoca vivipara, Lacertidae*) and the evolution of parity. Biological Journal of the Linnean Society 87:1-11.

Surget-Groba, Y., B. Heulin, C.-P. Guillaume, R. S. Thorpe, L. Kupriyanova, N. Vogrin, R. Maslak et al. 2001. Intraspecific phylogeography of *Lacerta vivipara* and the evolution of viviparity. Molecular Phylogenetics and Evolution 18:449-459.

Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. Global Change Biology 10:2020-2027.

Tinkle, D. W., and J. W. Gibbons. 1977. The distribution and evolution of viviparity in reptiles. Miscellaneous Publications, Museum of Zoology, University of Michigan No. 154:1-55.

Tokarz, R. R., and C. H. Summers. 2011. Stress and reproduction in reptiles, Pages 169-213 *in* D. O. Norris, and K. H. Lopez, eds. Hormones and Reproduction of Vertebrates, Academic Press.

Trenberth, K. E., A. Dai, R. M. Rasmussen, and D. B. Parsons. 2003. The changing character of precipitation. Bulletin of the American Meteorological Society 84:1205-+.

Trivers, R. L. 1972. Parental investment and sexual selection, Pages 136-207 *in* B. Campbell, ed. Sexual Selection and the descent of man 1871-1971. Chicago, Aldine Publishing Company.

Turchin, P. 1995. Population regulation: Old arguments and a new synthesis, Pages 19-40 *in* N. Cappuccino, and P. W. Price., eds. Population Dynamics: New Applications and Synthesis. NY, Academic Press.

Turchin, P., A. D. Taylor, and J. D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: An experimental test. Science 285:1068-1071.

Van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: Their influence on variation in life history tactics. American Naturalist 128:137-142.

van Nuland, G. J., and H. Strijbosch. 1981. Annual rhythmics of *Lacerta vivipara* Jacquin and *Lacerta agilis agilis* L. (Sauria, Lacertidae) in the Netherlands. Amphibia-Reptilia 2:83-95.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275:649-659.

Visser, M. E., F. Adriaensen, J. H. van Balen, J. Blondel, A. A. Dhondt, S. van Dongen, C. du Feu et al. 2003. Variable responses to large-scale climate change in European *Parus* populations. Proceedings of the Royal Society B: Biological Sciences 270:367-372.

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118:558-560.

Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2019-2024.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesank, T. J. C. Beebee, J.-M. Fromentin et al. 2002. Ecological responses to recent climate change. Nature 416:389 - 395.

Wallace, A. R. 1876, The geographical distribution of animals; with a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface. London, Macmillan & Co.

Wentz, F. J., L. Ricciardulli, K. Hilburn, and C. Mears. 2007. How much more rain will global warming bring? Science 317:233 - 235.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics 20:249-278.

Westphal, N. J., and A. F. Seasholtz. 2006. CRH-BP: The regulation and function of a phylogenetically conserved binding protein. Frontiers in Bioscience 11:1878-1891.

Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398-411.

Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann, and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biology 6:2621-2626.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in north american fishes: Implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196-2218.

Wolf, J. B., and M. J. Wade. 2009. What are maternal effects (and what are they not)? Philosophical Transactions of the Royal Society B: Biological Sciences 364:1107-1115.

Chapter I

Climate effects on life-history traits depend on population genetic characteristics

Cristina Romero-Diaz,
Merel Breedveld & Patrick S. Fitze

Submitted for publication (2016)

Abstract

Climatic change is expected to affect individual life-histories, and ultimately population dynamics, potentially increasing population vulnerability to extinction. While the importance of genetic diversity has been highlighted for adaptation and population persistence, it remains elusive whether responses of life-history traits to a given environmental condition depend on population genetic characteristics. Here we tested this hypothesis, using the polymorphic common lizard *Zootoca vivipara* as a model species. We simultaneously manipulated habitat humidity, a major climatic predictor of *Zootoca's* distribution, and adult male color morph frequency of 12 independent populations, and assessed their effects on individual life-history traits. Interactive effects of humidity and morph frequency had immediate effects on life-history traits of juveniles and yearlings (growth and body condition) and adults (survival), and delayed effects on offspring size. In yearlings, higher humidity led to larger female final body size, and lower humidity led to higher male compared to female survival. In juveniles and yearlings, several treatment effects were compensated over the course of the experiment. The results show that individual responses to environmental conditions depend on the population genetic characteristics, age class and sex, and that these affect intra- and inter-age class competition. This indicates that species' responses to changing environments, e.g., to climate change, are highly complex, and difficult to accurately reconstruct and predict without information on the genetic characteristics and demographic structure of populations.

Keywords: Age-structured populations, age class effects, life-history variation, *Zootoca vivipara*, humidity, color morph frequency.

Climatic, and more generally, environmental conditions can affect individual performance (e.g., growth rate, survival), population dynamics, and life-history evolution (Bjørnstad and Hansen 1994; Lindstrom 1999). Changes in environmental conditions may potentially destabilize populations (Lindström and Kokko 2002) and increase their vulnerability to extinction (Lande 1993; Melbourne and Hastings 2008). Population stability depends, among other factors, on genetic diversity, which facilitates adaptation and population persistence (Sgrò et al. 2011; Whiteley et al. 2015; but see Lande and Shannon 1996). Genetic characteristics of populations, such as genetic diversity *per se* (i.e., the genetic diversity within species, populations, or subpopulations), or the genotypic frequencies of polymorphisms, may affect the adaptive capacity of populations and species. This is because genetic morphs often differ in life-history strategies (reviewed in McKinnon and Pierotti 2010) and traits affecting population dynamics (San-Jose et al. 2014; Sinervo et al. 2008).

However, experiments determining whether and how the interaction between population genetic characteristics and environmental conditions affects life-history traits and demography are scarce (Bolton et al. 2015). Thus, whether the effects of environmental change on life-history traits and performance depend on the genetic characteristics of populations remains ambiguous, and so does their effects on the extinction risk of populations (Araújo et al. 2005; Lande and Shannon 1996; McMahon et al. 2011; Pacifici et al. 2015; Pertoldi et al. 2007; Sinclair et al. 2010).

The effects of environmental change also depend on whether and how an organism is able to cope with a change. Organisms may show an immediate response (e.g., Ergon et al. 2001), a delayed response, or they may not be able to respond and go extinct (Bellard et al. 2012; Charmantier et al. 2008; Hoffmann and Sgrò 2011; Visser 2008). Immediate responses frequently result from plasticity whereby organisms can cope with the changing environment or adapt behaviorally (Bertossa 2011; Charmantier et al. 2008). Delayed responses include (micro)evolutionary adaptation (Bellard et al. 2012; Visser 2008) and delayed life-history effects (Beckerman et al. 2002). The latter may result from environmental effects (e.g. effects of the maternal and/or offspring environment) on the expression of life-history traits (Lindstrom 1999; Mousseau and Fox 1998) and trade-offs among current and future reproduction (Le Galliard et al. 2008). Delayed life-history effects can also affect individual performance and give rise to cohort effects, including trans-stage and trans-generational effects, potentially affecting a population's response to changing environments (Benton et al. 2004; Benton et al. 2006). In summary, several studies suggest that the effects of environmental conditions and environmental change may depend, among others, on population genetic characteristics, age structure, and plasticity, but no unambiguous experimental evidence is yet available.

Here, we experimentally tested whether the effects of abiotic environmental conditions on life-history traits depend on the population's genetic characteristics. We used the common lizard (*Zootoca vivipara*) as a model species. The common lizard is a highly hydrophilic species and populations exhibit a pronounced age structure (Avery 1975a; Heulin 1985b). Adult males exhibit a genetic color polymorphism (Fitze et al. 2014; San-Jose et al. 2012; San-Jose et al. 2013) and the polymorphism frequency determines the population's genetic characteristics (Sinervo et al. 2007). *Z. vivipara*

occurrence is strongly associated with humidity (Ceirans 2007; Peñalver-Alcázar et al. 2016; Pilorge 1987) and climate change models predict a global increase in overall precipitation, mean and extreme temperature, and alteration of local precipitation patterns (IPCC 2013). Given the importance of humidity for *Z. vivipara*, we simulated environmental change by experimentally exposing lizards to different humidity regimes and crossed this treatment with a morph frequency treatment using a 2 x 3 design. Before the experiment started, lizards were maintained and clutches were incubated under standardized conditions. Thereafter, lizards were released in semi-natural populations (i.e., outdoor populations with natural vegetation, prey, and climatic conditions, in which lizards were enclosed and protected from predation; e.g., Le Galliard et al. 2008; Le Galliard et al. 2005b; San-Jose et al. 2014) with different humidity conditions and different morph frequencies. After one year, they were recaptured for egg laying and for quantifying treatment effects on individual life-history traits (namely, size and body condition at reproduction, growth rates, annual survival, reproductive and offspring traits). Conditions during egg laying and egg incubation were the same for all individuals/eggs. This experimental design allowed testing for immediate treatment effects on released lizards and for delayed effects on the newborns.

We predicted (1) significant effects of habitat humidity on life-history traits, especially of juveniles and yearlings, because they allocate most of their energy to growth and thus should be particularly susceptible to environmental conditions (Pilorge et al. 1987). If climatic effects depend on population genetic characteristics, we predicted (2) a significant interaction between habitat humidity and adult color morph frequency on individual life-histories. Moreover, we predicted that (3) inter-age class competition depends on the humidity and/or color morph frequency, and that effects will be most pronounced in the youngest age classes due to resource-based asymmetric competition (Massot et al. 1992). Specifically, we predicted that juveniles will be more affected than yearlings, and adults will be the least affected given that dominance interactions are size-dependent (Lecomte et al. 1994; Pilorge et al. 1987; San-Jose et al. 2016). Based on previous observational and experimental evidence (Bleu et al. 2013; Le Galliard et al. 2006; Lorenzon et al. 2001; Lorenzon et al. 1999; Marquis et al. 2008), we also predicted (4) delayed treatment effects on the offspring's phenotype. Particularly, positive effects of humidity on clutch size and hatchling size, presumably mediated

through increased habitat productivity (e.g., more available food) and/or a higher reproductive investment (Bleu et al. 2013; Le Galliard et al. 2006).

MATERIALS AND METHODS

Model species

The common lizard is a small, sexually dimorphic (e.g., females are longer than males, sexes differ in ventral coloration), ground-dwelling lacertid that preferentially inhabits hygrophilic and mesophilic habitats and its spatial distribution is linked with soil humidity (Braña 1996; Peñalver-Alcázar et al. 2016). *Z. vivipara* has a highly permeable skin, which increases the risk of hydric loss (Grenot et al. 1987) and its hydric balance is mainly controlled by environmental factors and behavioral regulation, i.e., by microhabitat selection or use (Grenot and Heulin 1990; Lorenzon et al. 1999). Water availability constrains growth and reproduction (Le Galliard et al. 2006; Lorenzon et al. 1999), litter size (Bleu et al. 2013), juvenile performance (Le Galliard et al. 2010) and reproductive performance (Marquis et al. 2008), including juvenile size at hatching (Le Galliard et al. 2006; Lorenzon et al. 2001; Marquis et al. 2008). The activity period lasts from March to October and reproduction begins immediately after females emerge from hibernation (Breedveld and Fitze 2015; Fitze et al. 2010). Most individuals attain sexual maturity in their second year of life and maturation depends on body size rather than age. The observed minimal reproductive body size varies between 40 - 45 mm (Bauwens 1999; Heulin 1985b). Juvenile mortality is considerably high (up to 90%) and once survived the first year, average lifespan is 4 - 5 years in males and 5 - 6 years in females (Avery 1975a). The reproductive system is polygynandrous and multiple paternity is common (Fitze et al. 2005). Females lay 1 to 3 clutches per year (Heulin et al. 1994; Horváthová et al. 2013; Roig et al. 2000) and once the clutch is laid, no parental care is provided. In Pyrenean populations, females lay on average 5 eggs per clutch (range 1-9). Adult *Z. vivipara* are socially dominant over yearlings, adults and yearlings over juveniles, and adult males over adult females (Pilorge et al. 1987).

In the Pyrenean populations, adult males, but not females (Arribas 2009), exhibit ventral color morphs that behave like a single locus with 3 alleles (white, *w*; yellow, *y*; and orange, *o*; Sinervo et al. 2007). Morphs can be classified using two color scores (namely, *o* and *w* score), which account for the number of putative color alleles (*o* score: 2 = *oo*; 1 = *yo*, *wo*; 0 = *yy*, *wy*, and *ww*; *w* score: 2 = *ww*; 1 = *wy*, *wo*; 0 = *yy*, *yo*, and *oo*; Sinervo et al. 2007). Color morphs differ visually and are

determined by differential carotenoid deposition (San-Jose et al. 2012; San-Jose et al. 2013), which is unaffected by carotenoid ingestion (Fitze et al. 2009; San-Jose et al. 2013), in line with genetic determination of color morphs (Fitze et al. 2014). Male color morphs exhibit alternative behavioral strategies and periodic frequency cycles (Sinervo et al. 2007). Females have whitish bellies and exhibit context-dependent mate choice (Fitze et al. 2010), choosing mate partners whose offspring survive best under the predominant adult color morph frequency in autumn (Fitze et al. 2014; San-Jose et al. 2014; Sinervo et al. 2007).

Experimental design

From May 2009 to June 2011, lizards originally captured in the Spanish central Pyrenees (Roncesvalles, Somport, and Formigal; "NE Spain" clade, Milá et al. 2013) were maintained under semi-natural conditions in 12 enclosures located at the field station 'El Boalar' near Jaca, Spain (Figure S2.1). Enclosures (100 m^2) were surrounded by galvanized metal walls and covered by nets, preventing lizards from escaping and avoiding terrestrial and avian predation. Each enclosure contained a patch of natural vegetation, two water ponds, and four stone piles providing natural food and water as well as basking sites and shelters. The hydric conditions were identical in all 12 enclosures until May 2010, when all lizards were recaptured. Thereafter lizards were released in enclosures (randomly with respect to the population of origin) attributed to different experimental treatments (see below and Figure S2.2). In each enclosure, 20 adults (males n = 8, females n = 12), 5 to 6 yearlings (males n = 2, females n = 3 or 4), and 18 to 20 newborn juveniles were introduced (population size: n = 43 - 46). The adult sex ratio, age structure and population density were similar to the average found across oviparous populations (Heulin et al. 1997).

Two treatments, adult male color-morph frequency ("CMF") and humidity treatment, were applied at the population level using a 3 x 2 factorial design. Four enclosures were biased towards orange (hereafter, orange biased: "Ob"), 4 towards yellow ("Yb"), and 4 towards white ("Wb") allele dominance (Figure S2.2). The 8 adult males released per enclosure (i.e., 16 alleles) matched an allelic proportion as close as possible to 2:1:1 (dominant allele: subdominant allele 1: subdominant allele 2; Figure S2.2). Male color morphs were scored by eye and verified using photographs (for further details see Sinervo et al. 2007).

Half of the enclosures of each CMF treatment were exposed to high ("H") humidity and the other half to low ("L") humidity (Figure S2.2). The level of humidity was manipulated using an

automatic irrigation system that uniformly irrigated each enclosure twice a day (i.e., at 9 a.m. and 5:30 p.m.). At each irrigation, enclosures belonging to the H treatment were sprinkled for 12, and those of the L treatment for 5, minutes. Each irrigation was split into two shifts (H: 6 and 6 minutes; L: 3 and 2 minutes of irrigation). The second shift started 2 and 9 minutes (H and L treatment, respectively) after the end of the first shift. This procedure guaranteed that in all enclosures 14 minutes passed between the start and end of the irrigation and thus lizards of all treatments were exposed to the same treatment length. From 2009 to May 2010 the humidity regime was between the L and H level of the humidity treatment: each enclosure was sprinkled for 8 minutes in the morning and 5 minutes in the afternoon.

The humidity of the enclosures without irrigation is below the common lizard's natural humidity requirements, allowing humidity manipulation within the species' natural range. The simulated H and L levels conformed to the highest and lowest 10-15 percentile of the humidity range found in natural populations of the Pyrenees (Peñalver-Alcázar et al. 2016). In every enclosure the humidity level was periodically measured (in June, July, August, April and May) by taking 5 soil core samples of identical volume from each enclosure and calculating average soil moisture content using a gravimetric method: m_{wet}-m_{dry}. Measurements of soil humidity included natural precipitation and it was significantly different between humidity treatments in all occasions (all $P < 0.05$). All lizards were individually marked by toe-clipping, weighted to the nearest mg and measured to the nearest mm. Lizards were randomly distributed among treatments (except with respect to adult male color morph) and there were no significant initial differences in snout-vent length (SVL) or body condition (BC; the residuals from the regression between body size and weight) among treatments and experimental populations (all $P > 0.360$).

Measurements of life-history traits

After June 2010, lizards were recaptured during two capture-recapture sessions (in August 2010 and September 2010), each consisting of three consecutive days of intensive captures with equal effort across time and enclosures. All captured individuals were identified, measured for SVL, weighted, photographed, and released back at the exact capture location the following morning. From May 23rd to June 8th 2011, the enclosures were completely emptied and captured individuals maintained in the laboratory. We recorded individual growth rate, SVL and BC at the end of the study, and annual survival.

Measurements of reproductive traits

All lizards were housed under the same standardized conditions in the laboratory. They were kept individually in *terraria* (20 x 15 x 15 cm) containing a shelter, a water pond, a rock for basking, and peat soil as substrate. Light and heat were provided by a 40W bulb following a 12h light: 12h dark photoperiod. Ultraviolet (UV) lamps provided UVB and UVA for two hours per day (12 a.m. – 2 p.m.) to facilitate calcium metabolism (San-Jose et al. 2014). Water was available *ad libitum* and prey items, *Galleria mellonella*, *Acheta domestica*, or *Lumbricus terrestris* were provided every other day. Terraria of females were inspected twice a day for laid clutches. Upon laying, clutch size (i.e., the number of eggs) and laying date were recorded and laid clutches were thereafter incubated individually in a constantly humid atmosphere at 21°C during the day (from 9 a.m. to 9 p.m.) and 19°C during the night (Heulin et al. 1997). On the day of hatching, offspring sex (determined by ventral scale count; Lecomte et al. 1992), SVL, tail length (to the nearest mm), and body mass (to the nearest mg) were recorded.

Statistics

Statistical analyses were performed in R (R 2.15.2) using packages nlme (Pinheiro et al. 2013), and lme4 (Bates et al. 2013). Life-history traits were analyzed for each age class (juveniles, yearlings, adults) and, where applicable, time period (release-August, August-September, September-June) separately using linear mixed models. To test for significant differences among age classes or time periods (i.e., treatment × age class, or treatment × time period interactions), models including either all age classes or all time periods were run (Table 2.1).

Humidity and CMF treatments, sex, and all first-order interactions were modeled as fixed effects, and initial SVL ("ISVL"; for juveniles: the SVL at hatching; for yearlings and adults: the SVL at the beginning of the experiment) or initial body condition ("IBC") as covariates, the latter only in BC analyses. Enclosure ID and, in models on juveniles, mother ID nested within enclosure ID were modeled as random effects. Hatching date was included as a covariate in the analyses of juvenile and offspring traits (i.e., SVL, BC and tail length at hatching).

Growth rate was defined as the difference in SVL between two capture events divided by the number of days passed ($\Delta SVL/\Delta Time$; e.g., Clobert et al. 2000; Le Galliard et al. 2010; Sorci et al. 1996a), excluding the number of days spent in hibernation (from the 1st of November to the 1st of March; e.g., Mugabo et al. 2010). "Final SVL" refers to the SVL and "final BC" to the BC

reached at the end of the study (June 2011), i.e., during the reproductive season. In the analyses of final SVL and final BC, "time" accounted for the total time spent inside the populations from release to recapture. Relative clutch size ("Rclsize"; the residuals of the regression of clutch size on female SVL), a measure of a female's reproductive effort (Massot et al. 2011), was added as a covariate in offspring models, accounting for female body size-independent differences in clutch size. Offspring sex ratio was calculated as the number of male hatchlings divided by the number of hatchlings.

Two adjacent enclosures suffered abnormally high mortality due to invasion of terrestrial predators and within one month only few individuals remained alive (4 out of 43, and 5 out of 43, respectively). Consequently, we excluded both populations from the analyses. Offspring of undetermined sex (i.e., equivocal sex attribution) were excluded from offspring analyses (n = 37). The average recapture probability of surviving yearlings and adults was 87% and 90% in juveniles. Thus, annual survival probability was analyzed using generalized linear mixed-effects models with binomial error distribution and a logit link. This model included the same parameters as the above-described models.

Model simplification was performed following Zuur et al. (2009) and likelihood ratio tests were used to test parameter significance. In the minimal adequate model, the significance of the main effects was tested using ANOVA type III tests. *P* values for random effects were corrected for testing on the boundary (Zuur et al. 2009). In all Gaussian models, the assumptions of independence, normality and homoscedasticity were verified on the residuals. In some models heteroscedasticity existed and was taken into account by specifying a *varIdent* structure. All non-Gaussian models were tested for overdispersion, and no evidence for overdispersion existed. For significant factors containing more than two groups, *post hoc* tests were performed using pairwise contrasts and Holm-Bonferroni corrections were applied to account for multiple comparisons (Holm 1979). The significance level was set at $P = 0.05$ and estimates ± standard errors are provided.

RESULTS

Treatment effects on life-history traits

Effects on body size and growth

Final SVL was significantly affected by a triple interaction between humidity, sex, and age class ($\chi^2_2 = 8.38$, $P = 0.015$; Table 2.1) and it positively correlated with ISVL ($\chi^2_1 = 76.29$, $P < 0.001$). Only in

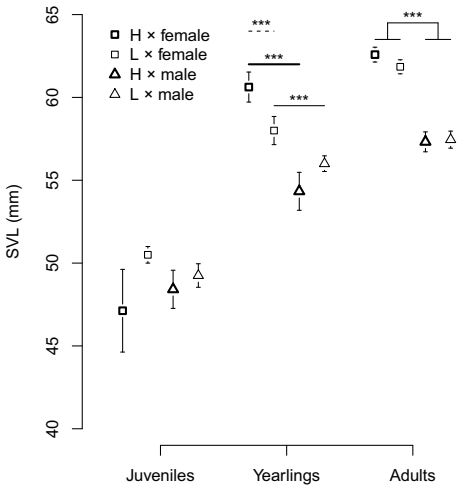


Figure 2.1 Final snout-vent length (SVL) of juveniles, yearlings and adults by humidity treatment (H: High; L: Low) and sex. Means ± SE are given. Horizontal bars depict main effects (i.e., sex differences) or *post hoc* contrasts, and asterisks indicate statistical significance: *** $P < 0.001$.

yearlings, the interaction between humidity and sex was significant (Figure 2.1). No other effects were found ($P \geq 0.120$).

Juveniles

We found no significant treatment effects (Table 2.1) nor differences between sexes on juvenile final SVL (Table S2.1). ISVL and time inside the enclosure positively correlated with final SVL ($\chi^2_1 = 6.05$, $P = 0.014$ and $\chi^2_1 = 11.11$, $P < 0.001$, respectively). There was a significant interaction between humidity, CMF, and time period on juvenile growth rate ($\chi^2_4 = 16.65$, $P = 0.002$; Table 2.1). From release to August and from September to June, the interaction humidity by CMF significantly affected growth rate (Table 2.2), showing that individuals belonging to different CMF treatments responded differently to humidity (see Figure 2.2*a*). Growth rate differences from release to August were balanced by the differences from September to June, leading to no treatment effects on final SVL (Table S2.1; for more details see appendix A1). In addition, juveniles grew faster from August to September in L compared to H (Table 2.2).

Sex and hatching date effects on juvenile growth rate differed among time periods (Table S2.2). Males grew significantly faster than females from release to August, while females grew faster than males from September to June (Table 2.2). Hatching date negatively correlated with growth rate from release to August but it positively correlated from September to June (Table 2.2). In both cases, the opposing growth patterns led to no significant differences in juvenile final SVL (Figure 2.1).

Yearlings

Yearling final SVL was significantly affected by an interaction between humidity and sex ($\chi^2_1 = 8.46$, $P = 0.004$; Figure 2.1). Females in H humidity had larger final SVL than females in L (*Post hoc*: $\chi^2_1 = 15.49$, $P < 0.001$), while males were unaffected. As in juveniles, ISVL positively correlated with final SVL ($\chi^2_1 = 24.23$, $P < 0.001$).

Table 2.1 Summary of treatment effects on measured life-history traits of common lizards. Shown are the results of models including all time periods or age classes, and models for each time period and/or age class separated. Significant (+) and non-significant (○) treatment effects are reported. Significant interactions are indicated by superscripts (see notes: *; †; ‡; §), the locations of the original analyses (below the measured traits), and of the direction of the effects are provided. Symbol size depicts the level of statistical significance: + $P < 0.05$; + $P < 0.01$; + $P < 0.001$.

Life-history trait	Treatment	All time periods	rel-Aug	Aug-Sept	Sept-Jun	Direction
Juvenile growth (Table S2.2 / 2.2)	CMF	$+^{*\dagger}$	$+^{\dagger}$	○	$+^{\dagger}$	Fig. 2.2*a*
	Humidity	$+^{*\dagger}$	$+^{\dagger}$	+	$+^{\dagger}$	
Yearling growth (Table S2.3 / 2.2)	CMF	$+^{*\S}$	+	$+^{\S}$	○	Fig. 2.2*c*, Fig. 2.2*b*
	Humidity	$+^{*\S}$	○	$+^{\S}$	○	
Adult growth (in text)	CMF	○	○	○	$+^{\S}$	in text
	Humidity	○	○	○	○	
		All ages	Juveniles	Yearlings	Adults	Direction
Final SVL (in text / Table S2.1)	CMF	○	○	○	○	Fig. 2.1
	Humidity	$+^{\ddagger\S}$	○	$+^{\S}$	○	
Final BC (in text)	CMF	$+^{\ddagger\dagger}$	$+^{\dagger}$	+	○	Fig. 2.3
	Humidity	$+^{\ddagger\dagger}$	$+^{\dagger}$	○	○	
Survival (in text)	CMF	$+^{\ddagger\dagger}$ / $+^{\S}$	$+^{\S}$	+	$+^{\dagger}$	Fig. 2.4
	Humidity	$+^{\ddagger\dagger}$ / $+^{\S}$	○	○	$+^{\dagger}$ / $+^{\S}$	

*Interaction with time period
†Interaction between treatments
§Interaction with sex
‡Interaction with age class

There was a significant interaction between humidity, sex and time period (χ^2_2 = 7.95, P = 0.019; Table 2.1) on yearling growth rate. Only from August to September, humidity effects depended on the sex (Table 2.2; Figure 2.2*b*). Females in H humidity grew faster than females in L, while no differences existed in males. There was also a significant interaction between CMF, sex and time period on growth rate (Table 2.1). The interaction between CMF and sex affected growth rate only from August to September (Table 2.2; Figure 2.2*c*). In Yb, females grew faster than males (*Post hoc*: χ^2_1 = 7.61, P = 0.017), while in Wb, males grew faster than females. In contrast, from release to August, females in Wb populations grew faster than males (Figure 2.2*c*). Growth differences from

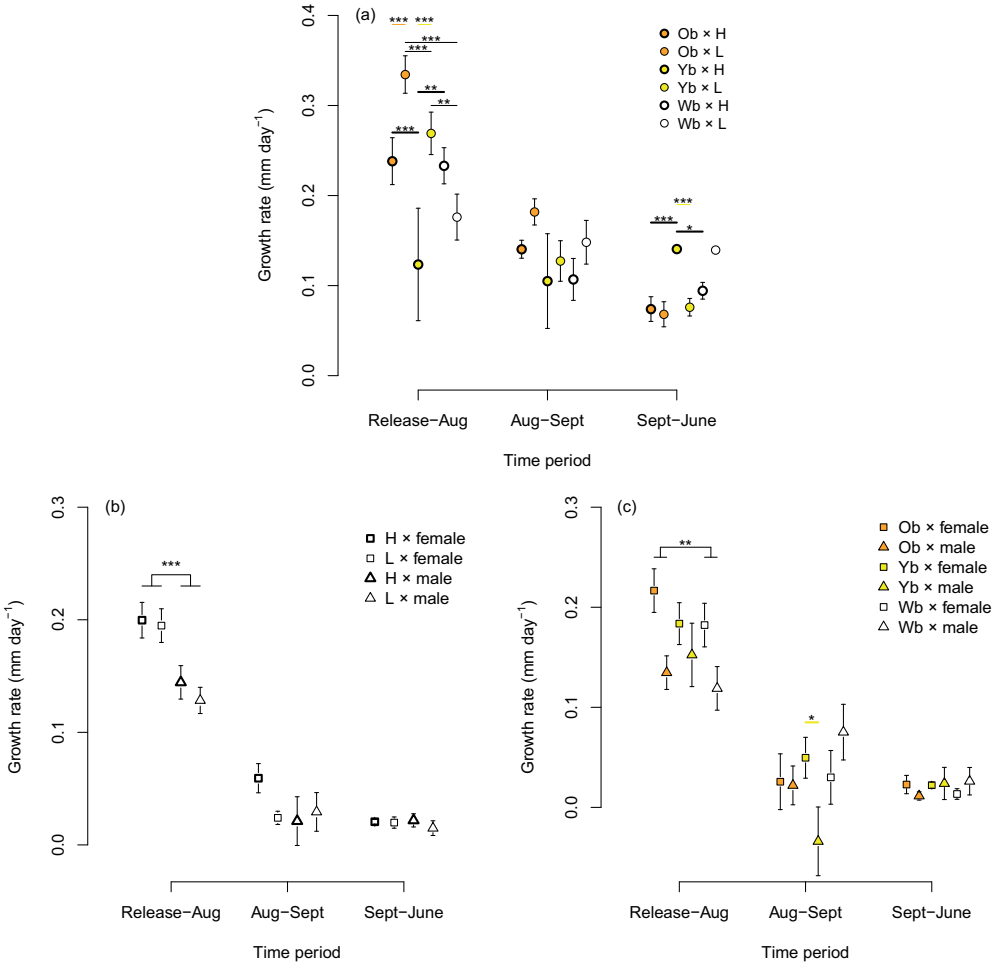


Figure 2.2 Juvenile growth rate by color morph frequency (CMF; orange-, yellow-, and white-biased) and humidity treatment (a; H: High humidity; L: Low humidity); yearling growth rate by humidity and sex (b) and CMF and sex (c) for each of the three time periods. Shown are means ± SE, horizontal bars depict main effects (sex and CMF differences) or *post hoc* contrasts, and asterisks indicate the level of statistical significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

release to August balanced by growth differences from August to September, leading to no CMF × sex effect on final SVL (for further details see appendix A2). Moreover, CMF affected growth rate from release to August (Table 2.2). Yearlings in Ob populations grew faster than yearlings in Wb populations ($Z = 2.96$, $P = 0.009$; Figure 2.2c) and this difference was compensated by slightly higher growth rates of Wb compared to Ob populations from August to September, leading to no CMF effect on final SVL (Table 2.1).

Table 2.2 Treatment effects on juvenile and yearling growth rates (mm day^{-1}) measured over three time periods: release-August, August-September, September-June. Results of likelihood ratio tests are shown and the minimal adequate model is depicted in bold. Plain values correspond to the values before backward elimination.

Effects	release-August			August-September			September-June		
	χ^2	*df*	*P*	χ^2	*df*	*P*	χ^2	*df*	*P*
JUVENILES									
Fixed									
CMF	**21.07**	**2**	**<0.001**	5.79	2	0.055	**132.30**	**2**	**<0.001**
Humidity	**25.99**	**1**	**<0.001**	**4.88**	**1**	**0.027**	**0.170**	**1**	**0.680**
CMF × humidity	**17.63**	**2**	**<0.001**	1.08	2	0.634	**19.65**	**2**	**<0.001**
Sex	**6.86**	**1**	**0.009**	0.20	1	0.991	**12.52**	**1**	**<0.001**
CMF × sex	0.32	2	0.851	0.19	2	0.926	†	†	†
Humidity × sex	1.30	1	0.255	0.27	1	0.556	1.98	1	0.159
ISVL (mm)	0.62	1	0.432	1.05	1	0.380	**16.01**	**1**	**<0.001**
Hatching date (days)	**41.85**	**1**	**<0.001**	0.70	1	0.268	**21.05**	**1**	**<0.001**
Random									
Enclosure ID	**0.26**	**2**	**0.438**	**1.69**	**2**	**0.214**	**2.08**	**2**	**0.177**
Mother ID[Enclos. ID]	**0.32**	**1**	**0.286**	**0.76**	**1**	**0.191**	**<0.01**	**1**	**0.500**
YEARLINGS									
Fixed									
CMF	**7.45**	**2**	**0.024**	1.57	2	0.455	3.67	2	0.160
Humidity	0.24	1	0.625	**3.89**	**1**	**0.048**	2.27	1	0.132
CMF × humidity	1.41	2	0.494	5.43	2	0.066	1.53	2	0.464
Sex	**18.50**	**1**	**<0.001**	**2.76**	**1**	**0.096**	0.61	1	0.434
CMF × sex	<0.01	2	0.998	**9.24**	**2**	**0.010**	2.250	2	0.325
Humidity × sex	0.11	1	0.735	**4.51**	**1**	**0. 034**	<0.01	1	0.948
ISVL (mm)	**43.14**	**1**	**<0.001**	**4.49**	**1**	**0.034**	**7.29**	**1**	**0.007**
Humidity × ISVL	0.35	1	0.555	**4.54**	**1**	**0.033**	2.38	1	0.123
Random									
Enclosure ID	**0.17**	**2**	**0.458**	**<0.01**	**2**	**0.500**	**<0.01**	**2**	**0.500**

† not possible to model since not enough juveniles survived in each of the combinations.

Finally, there was also a significant triple interaction between humidity treatment, ISVL and time period on growth rate (Table S2.3). From release to August and from September to June the correlation was more negative in L than in H (although humidity × ISVL was not statistically significant), while from August to September it was significantly more negative in H (Table 2.2), leading to a non-significant humidity × ISVL interaction on final SVL (Table S2.1).

Adults

In adults, we found no significant treatment effects on final SVL (all $P \geq 0.122$; Table 2.1). Final SVL of males was shorter than that of females ($\chi^2_1 = 28.90$, $P < 0.001$; Figure 2.1), and it positively correlated with ISVL ($\chi^2_1 = 57.97$, $P < 0.001$). Neither treatments nor their interaction significantly affected adult growth rate (Table 2.1). However, a CMF by sex interaction affected growth from September to June; females in Yb grew faster than females in Ob ($\chi^2_1 = 6.83$, $P = 0.045$) and Wb ($\chi^2_1 = 9.12$, $P = 0.015$). Growth rate was also affected by the interactions between sex and time period ($\chi^2_2 = 30.45$, $P < 0.001$) and ISVL and time period ($\chi^2_2 = 62.58$, $P < 0.001$). Females grew faster than males from release to August ($\chi^2_1 = 45.57$, $P < 0.001$), but not in the other two periods (August-September: $\chi^2_1 = 45.57$, $P = 0.294$; September-June: $\chi^2_1 = 1.44$, $P = 0.229$). In turn, ISVL negatively correlated with growth rate from release to August and August to September ($\chi^2_1 = 98.98$, $P < 0.001$, and $\chi^2_1 = 9.53$, $P < 0.001$, respectively), but not from September to June.

Effects on body condition

Final BC was affected by a significant triple interaction between humidity, CMF and age class ($\chi^2_4 = 14.01$, $P = 0.007$; Table 2.1; Figure 2.3). The interaction between treatments affected juveniles ($\chi^2_2 = 12.81$; $P = 0.002$), but not yearlings or adults ($P \geq 0.230$; Table 2.1).

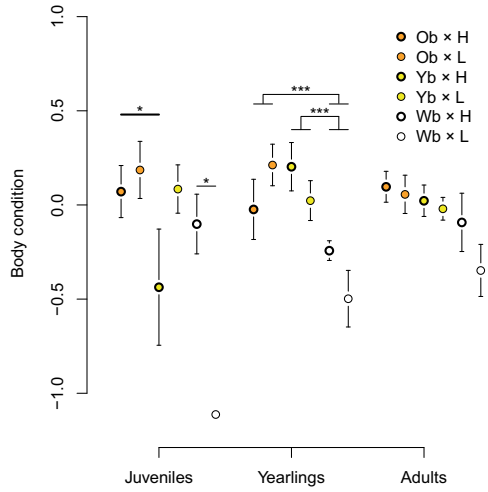


Figure 2.3 Final body condition (BC) of juveniles, yearlings and adults by color morph frequency (CMF; orange-, yellow-, and white-biased are colored with their respective colors) and humidity treatment (High humidity: bold and Low humidity: plain circles). Means ± SE are given. Horizontal bars depict significant main effects (CMF differences) or *post hoc* contrasts and asterisks statistical significance: * $P < 0.05$; *** $P < 0.001$.

Final BC was also affected by an interaction between sex and age class (χ^2_2 = 13.82, P = 0.001), an interaction between time spent in the enclosure and age class (χ^2_4 = 6.50, P = 0.039), and it was positively correlated with IBC (χ^2_1 = 6.23, P = 0.013). Final BC differed between sexes in juveniles, but not in yearlings or adults (all P > 0.281) and time in the enclosure negatively correlated with final BC of yearlings (χ^2_1 = 5.09, P = 0.024), but not of juveniles or adults (all P > 0.445).

Juveniles

In Wb populations, juveniles in H humidity showed higher final BC than those in L (*Post-hoc*: χ^2_1 = 7.10, P = 0.023; Figure 2.3). In Yb populations, juveniles tended to have higher BC in L than in H humidity (χ^2_1 = 4.19, P = 0.081), while Ob populations were unaffected (P = 0.270). Moreover, in H humidity, final BC of juveniles of Ob populations was significantly higher than of Wb populations, and tended to be higher than Yb populations (χ^2_1 = 7.41, P = 0.039; χ^2_1 = 6.02, P = 0.071, respectively; Figure 2.3). In L humidity, juveniles of Wb populations had lower body condition than those of Yb and Ob populations, but these differences were not statistically significant (all $P \geq 0.134$). In addition, females had lower final BC than males (χ^2_1 = 16.41, P < 0.001).

Yearlings

CMF significantly affected yearling final BC (χ^2_2 = 10.99, P = 0.004). In Ob and Yb populations final BC was higher than in Wb populations (*Post-hoc*: Z = 4.27, P < 0.001 and Z = 3.82, P < 0.001, respectively; Figure 2.3). There was a significant interaction between humidity, CMF, and time period on body condition change (Table S2.4), revealing different humidity by CMF effects in different time periods. Given the absence of an interaction between humidity and CMF on final BC (P = 0.230), interactive treatment effects were compensated over the course of the experiment.

Effects on survival

Survival was affected by a significant interaction between humidity, CMF, and age class (χ^2_4 = 10.17, P = 0.038; Table 2.1; Figure 2.4). *Post-hoc* contrasts showed that adults in H humidity survived worse in Wb compared to Ob and Yb populations (Z = 3.73, P < 0.001; Z = 3.07, P = 0.006, respectively; Figure 2.4*c*), while no humidity differences existed in L, juveniles, and yearlings (Figure 2.4*a, b*). The interactions between CMF and sex (χ^2_2 = 8.79, P = 0.012), and humidity and sex (χ^2_1 = 6.30, P = 0.012) were also significant (Table 2.1). Males survived worse in Wb populations compared to Ob (χ^2_1 = 15.42, P < 0.001) and Yb (χ^2_1 = 11.64, P = 0.003)

populations, and they survived better than females in Ob populations (χ^2_1 = 8.81, P = 0.009). Moreover, in L humidity males survived better than females (χ^2_1 = 10.11, P = 0.003), while no differences existed in H (χ^2_1 = 0.18, P = 0.668).

Reproductive success

A total of 71 females laid a clutch. Average clutch size was 5.37 ± 0.16 eggs, and 241 juveniles hatched successfully (i.e., alive; males: n = 124; females: n = 80; undetermined sex: n = 37). We found no significant differences in clutch size among treatments or interactions with treatments (all P > 0.570). Clutch size positively correlated with female SVL (χ^2_1 = 9.02, P = 0.003).

Offspring traits

Offspring sex ratio was on average 0.61 (i.e., male biased), and was affected by CMF (χ^2_2 = 6.30, P = 0.043). *Post hoc* tests revealed male biased sex ratios in Ob and Yb and female biased sex ratios in Wb populations (Z = 2.31, P = 0.05; Z = 2.33, P = 0.049, respectively; Figure S2.3).

SVL of hatchlings was significantly affected by an interaction between humidity and CMF (Table S2.5; Figure S2.4). *Post hoc* tests showed that in Ob populations, hatchlings of mothers from H humidity were larger than those of mothers from L humidity (0.91 mm; χ^2_1 = 5.75, P = 0.049). In L, offspring of Ob mothers were significantly shorter than those of Wb (1.50 mm; χ^2_1 = 7.86, P =

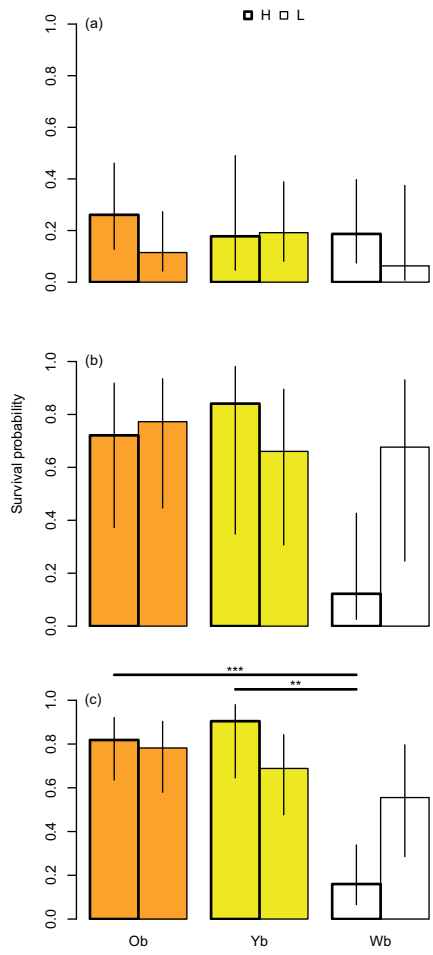


Figure 2.4 Interaction of color morph frequency (CMF; orange-, yellow-, and white-biased) and humidity (H: High; L: Low) on annual survival probability of all three age classes: juveniles (a), yearlings (b) and adults (c). Shown are mean expected survival probabilities ± 95% CI. Horizontal bars depict *post hoc* contrasts and asterisks indicate statistical significance: ** P < 0.01; *** P < 0.001.

0.025) or Yb mothers (1.40 mm; χ^2_1 = 11.77, P = 0.004). Males and females differed in size at hatching (Table S2.5); females were on average 1.74 ± 0.98 mm longer than males irrespective of treatment. Additionally, Rclsize and hatching date were negatively correlated with the progeny's SVL, the latter showing that early hatching juveniles were larger than later hatched juveniles.

Tail length at hatching was unaffected by treatments but it differed between sexes (Table S2.5). Males had 0.610 ± 0.030 mm longer tails than females. Neither Rclsize nor hatching date affected tail length. Similarly, offspring body condition at hatching was unaffected by treatments but it differed between sexes (Table S2.5). Males exhibited higher body condition than females. Additionally, tail length and body condition at hatching positively correlated.

DISCUSSION

Using an experimental approach, we tested whether and how environmental conditions and population genetic characteristics affect life-history traits, which are closely tied to demographic parameters, and thus alter the dynamics of populations (Bjørnstad and Hansen 1994). Our results reveal effects of habitat humidity on juvenile growth (prediction 1), and interactive effects of habitat humidity and population genetic characteristics (i.e., adult color morph frequency) on growth and body condition of juveniles and yearlings (2), pointing to treatment effects on inter-age class competition (3). We also found interactive effects on adult survival and delayed interactive treatment effects on offspring traits (4)(Table 2.1). These results show that abiotic environmental conditions and population genetic characteristics are immediate and delayed (parentally-derived) sources of inter- and intra-age class variation in life-history traits, and thus that they influence the dynamics of populations (Bolnick et al. 2011; Lindstrom 1999).

Genetic variability (e.g., in terms of genotype diversity and frequency) is thought to favor population persistence and resilience via evolutionary rescue (Whiteley et al. 2015). Color polymorphic species are considered to be less vulnerable against changes in selective regimes, e.g., resulting from climate change, on account of their higher genetic variability and enhanced evolutionary potential (Forsman et al. 2008). However, the genetic architecture of many color polymorphisms is based on clusters of loci where color is linked with other traits, potentially constraining trait divergence (Bolton et al. 2015; McKinnon and Pierotti 2010; Wellenreuther et al. 2014) and thus the

role of population genetic characteristics in population stability is unclear.

Moreover, it has been suggested that genetic characteristics are of lesser importance to short-term population viability, although they might be crucial in the long-term (Lande 1988). In contrast to this suggestion, here we experimentally demonstrate that environmental effects depend on the genetic characteristics of a population (i.e., morph frequency) and that their interaction affects life-history traits, demography, and thus short-term population dynamics. For example, the effects of habitat humidity on adult survival depended on the morph frequency (Table 2.1; Figure 2.4*c*). In H humidity, Wb populations showed reduced adult survival compared to Ob and Yb populations. Because juvenile mortality is characteristically high, recruitment alone cannot compensate a significant drop in adult survival, putting these populations at risk (Bestion et al. 2015). Thus, population genetic characteristics can help predicting the impact of environmental change on local dynamics of *Z. vivipara* populations. Furthermore, close natural populations of *Z. vivipara* are often synchronous with respect to color morph phase (Sinervo et al. 2007) and thus neighboring populations may share a similar fate in response to environmental change, with consequences for meta-population dynamics. These results agree with earlier studies suggesting that population genetic characteristics influence the demographic trajectory of populations (e.g., in butterflies, Hanski and Saccheri 2006; in killifish, Leips et al. 2000; in moths, Nokelainen et al. 2013), and thus may be more relevant to short-term population dynamics than previously thought.

Our results also revealed plastic compensatory patterns (Charmantier et al. 2008), in line with flexible life-history strategies that allow to compensate for immediate effects of adverse conditions later in life (Le Galliard et al. 2008; Le Galliard et al. 2010; Lorenzon et al. 2001; Sorci et al. 1996a). For instance, humidity by CMF effects on early growth of juveniles (i.e., from release to August) and body condition change in yearlings were compensated over the course of the experiment, resulting in no interactive effects on final body size and body condition (Table 2.1). *A priori* this ability confers high potential for adaptation and resilience against unfavorable environmental changes. Additionally, treatments had delayed effects on offspring body size, an important determinant of age at maturation (Stearns 1992) and asymptotic body size (Fitze and Le Galliard 2008), the latter predicting reproductive success. This suggests that mothers may prepare

offspring for the conditions they will experience (Mousseau and Fox 1998), for instance, through offspring sex-ratio (Maślak et al. 2010) or juvenile body size adjustment, which may constitute another mechanism of delayed compensation (see Le Galliard et al. 2008).

Treatment effects also differed between sexes and age classes (Table 2.1; Figures 2.1-2.4). Sex differences are in line with sex-specific selective pressures (Pilorge et al. 1987), alternative life-history strategies (Massot et al. 1992) and different environmental sensitivity between the sexes (Lindstrom 1999). In yearlings, humidity affected growth rates and final SVL of females, but not of males (Table 2.1; Figures 2.1, 2.2*b*), and no treatment by sex effects existed on growth rates and SVL in juveniles and adults. Smaller final SVL of yearling females in L is in line with reduced food availability and variability in L humidity conditions (Chikoski et al. 2006; Ferguson 2004), and with slower growth rates induced by lower humidity *per se* (Lorenzon et al. 1999). Moreover, this sex-specific treatment effect is in line with higher energetic demands of females compared to males, due to their larger body sizes (Hulbert and Else 2004), pointing to increased susceptibility to environmental conditions of females. Given that SVL affects the timing of recruitment, a key demographic parameter contributing to variation in population growth (Coulson et al. 2005), humidity effects on SVL of female yearlings directly affect population dynamics and sexual selection (Fitze and Le Galliard 2008). Interestingly, sex and morph frequency-dependent sex differences in growth were compensated over the course of the experiment in juveniles and yearlings, respectively. In contrast, males of all age classes survived better in L humidity populations than females, while no differences existed in H. This indicates that in drier conditions, sex ratios of *Z. vivipara* populations will skew towards males due to higher male survival and later female recruitment, leading to an increase in male sexual harassment, reduced female survival, and eventually, to population collapse (Le Galliard et al. 2005c).

Differences in treatment effects among age classes agreed with the inter-age class competition hierarchy (adult dominance over yearlings, and older-age-class dominance over juveniles; Lecomte et al. 1994; Pilorge et al. 1987) since adults were the least affected while yearlings and juveniles were strongly affected by treatments (Table 2.1). CMF effects arise through differences in competition between adult males and the other age classes/sex (note: only adult morph frequency differed among CMF

treatments, but neither the number of lizards nor their characteristics), and thus treatment by age class effects are in line with dominance interactions based on resources, where the competitively superior individuals restrain the energy intake of the competitively inferior individuals if the resources are limited (Beckerman et al. 2003; De Roos and Persson 2003; Nicholson 1954). CMF by humidity interactions thus reveal an interplay between ecological conditions and intra- (in adults) or inter-age class competition (Mugabo et al. 2011; Mugabo et al. 2010). More generally, demographic changes in age and sex structure (i.e., sex-ratios) affect intra- and inter-age class competition and population effective size (Lande 1988), which can also importantly affect population dynamics and viability (Clutton-Brock and Parker 1995).

In conclusion, here we experimentally show that population responses to environmental change depend on the population genetic characteristics, and on its age-, and sex-structure, revealing their complexity. While some effects induced by environmental conditions could be compensated through behavioral short-term adaptation (e.g., plastic compensation patterns of differences in initial growth), others may threat population viability (e.g., alteration of demographic structure and morph frequency cycles). Since the genetic characteristics and the age- and sex-structures of a population generally vary over a species' distribution range (Corl et al. 2010; McLean and Stuart-Fox 2014), predicting species' responses to climatic change might be more challenging than previously thought (Bellard et al. 2012; Dawson et al. 2011; IPCC 2013; McMahon et al. 2011; Parmesan 2006). Our results suggest that a lack of data on genetic characteristics and demographic structure of local populations may importantly compromise the conservation of biodiversity, as well as the understanding of a species' evolutionary history.

Acknowledgements. We thank M. Peñalver-Alcázar, L. Ros Vicente and A. M. Prieto for assistance in the field and L. M. San-Jose for providing background knowledge. C.R.D. was supported by the Spanish Ministry of Education (FPU program), grant number AP2009-0350. M.C.B. was supported by a Ph.D. grant (JAEPre_09_01372) from the Consejo Superior de Investigaciones Científicas (CSIC) co-financed by the European Social Fund Project. Funds were provided by the Spanish Ministry of Education and Science (CGL2008-01522 and CGL2012-32459 to P.S.F) and the Swiss National Science Foundation (PPOOP3_128375, PP00P3_152929/1 to P.S.F). The capture and handling of lizards was conducted under the license provided by the Gobierno de Aragón (Ref: LC/ehv 24/2010/105 & 106) and Gobierno de Navarra. The conducted study complies with current Spanish laws and with ASAB/ABS Guidelines for the Treatment of Animals in Behavioral Research.

REFERENCES

Araújo, M. B., R. J. Whittaker, R. J. Ladle, and M. Erhard. 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14:529-538.

Arribas, O. J. 2009. Morphological variability of the Cantabro-Pyrenean populations of *Zootoca vivipara* (Jacquin, 1787) with description of a new subspecies (Squamata: Sauria: Lacertidae). Herpetozoa 21:123-146.

Avery, R. A. 1975a. Age-structure and longevity of Common lizard (*Lacerta vivipara*) populations. Journal of Zoology 176:555-558.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-4. http://CRAN.R-project.org/package=lme4.

Bauwens, D. 1999. Life-history variation in lacertid lizards. Natura Croatica 8:239-252.

Beckerman, A. P., T. G. Benton, C. T. Lapsley, and N. Koesters. 2003. Talkin' 'bout my generation: environmental variability and cohort effects. American Naturalist 162:754-767.

Beckerman, A. P., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology & Evolution 17:263-269.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365-377.

Benton, T. G., T. C. Cameron, and A. Grant. 2004. Population responses to perturbations: predictions and responses from laboratory mite populations. Journal of Animal Ecology 73:983-995.

Benton, T. G., S. J. Plaistow, and T. N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B: Biological Sciences 273:1173-1181.

Bertossa, R. C. 2011. Morphology and behaviour: functional links in development and evolution Introduction. Philosophical Transactions of the Royal Society B-Biological Sciences 366:2056-2068.

Bestion, E., A. Teyssier, M. Richard, J. Clobert, and J. Cote. 2015. Live fast, die young: Experimental evidence of population extinction risk due to climate change. PLoS Biology 13:e1002281.

Bjørnstad, O. N., and T. F. Hansen. 1994. Individual variation and population dynamics. Oikos 69:167-171.

Bleu, J., J.-F. Le Galliard, P. S. Fitze, S. Meylan, J. Clobert, and M. Massot. 2013. Reproductive allocation strategies: a long-term study on proximate factors and temporal adjustments in a viviparous lizard. Oecologia 171:141-151.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf et al. 2011. Why intraspecific trait variation

matters in community ecology. Trends in Ecology & Evolution 26:183-192.

Bolton, P. E., L. A. Rollins, and S. C. Griffith. 2015. The danger within: the role of genetic, behavioural and ecological factors in population persistence of colour polymorphic species. Molecular Ecology 24:2907-2915.

Braña, F. 1996. Sexual dimorphism in lacertid lizards: Male head increase vs female abdomen increase? Oikos 75:511-523.

Breedveld, M. C., and P. S. Fitze. 2015. A matter of time: delayed mate encounter postpones mating window initiation and reduces the strength of female choosiness. Behavioral Ecology and Sociobiology 69:533-541.

Ceirans, A. 2007. Microhabitat characteristics for reptiles *Lacerta agilis*, *Zootoca vivipara*, *Anguis fragilis*, *Natrix natrix*, and *Vipera berus* in Latvia. Russian Journal of Herpetology 14:172-176.

Clobert, J., A. Oppliger, G. Sorci, B. Ernande, J. G. Swallow, and T. G. Jr. 2000. Trade-offs in phenotypic traits: Endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. Functional Ecology 14:675–684.

Clutton-Brock, T. H., and G. A. Parker. 1995. Sexual coercion in animal societies. Animal Behaviour 49:1345-1365.

Corl, A., A. R. Davis, S. R. Kuchta, and B. Sinervo. 2010. Selective loss of polymorphic mating types is associated with rapid phenotypic evolution during morphic speciation. Proceedings of the National Academy of Sciences of the United States of America 107:4254-4259.

Coulson, T., J. M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology 74:789-801.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800-803.

Chikoski, J. M., S. H. Ferguson, and L. Meyer. 2006. Effects of water addition on soil arthropods and soil characteristics in a precipitation-limited environment. Acta Oecologica-International Journal of Ecology 30:203-211.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond Predictions: Biodiversity conservation in a changing climate. Science 332:53-58.

De Roos, A. M., and L. Persson. 2003. Competition in size-structured populations: mechanisms inducing cohort formation and population cycles. Theoretical Population Biology 63:1-16.

Ergon, T., X. Lambin, and N. C. Stenseth. 2001. Life-history traits of voles in a fluctuating population respond to the immediate environment. Nature 411:1043-1045.

Ferguson, S. H. 2004. Does predation or moisture explain distance to edge distribution of soil arthropods? The American Midland Naturalist 152:75-87.

Fitze, P. S., J. Cote, and J. Clobert. 2010. Mating order-dependent female mate choice in the poligynandrous common lizard *Lacerta vivipara*. Oecologia 162:331-341.

Fitze, P. S., J. Cote, L. M. San-Jose, S. Meylan, C. Isaksson, S. Andersson, J. M. Rossi et al. 2009. Carotenoid-based colours reflect the stress response in the common lizard. PLoS ONE 4:1-10.

Fitze, P. S., V. González Jimena, L. M. San-Jose, B. Heulin, and B. Sinervo. 2014. Frequency-dependent sexual selection with respect to offspring fitness returns is consistent with predictions from rock-paper-scissors dynamics in the European common lizard. Frontiers in Ecology and Evolution 2:77.

Fitze, P. S., and J.-F. Le Galliard. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. Ecology Letters 11:432-439.

Fitze, P. S., J.-F. Le Galliard, P. Federici, M. Richard, and J. Clobert. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. Evolution 59:2451-2459.

Forsman, A., J. Ahnesjo, S. Caesar, and M. Karlsson. 2008. A model of ecological and evolutionary consequences of color polymorphism. Ecology 89:34-40.

Grenot, C., and B. Heulin. 1990. Sur la plasticité ecophysiologique du lézard vivipare, *Lacerta vivipara* (*Reptilia, Lacertidae*). Bulletin de la Societe Herpetologique de France 54:1-22.

Grenot, C., B. Heulin, T. Pilorge, M. Khodadoost, A. Ortega, and Y. P. Mou. 1987. Water budget in some populations of the European common lizard, *Lacerta vivipara* Jacquin. Functional Ecology 1:131-138.

Hanski, I., and I. Saccheri. 2006. Molecular-level variation affects population growth in a butterfly metapopulation. PLoS Biology 4:719-726.

Heulin, B. 1985b. Maturité sexuelle et âge à la première reproduction dans une population de plaine de *Lacerta vivipara*. Canadian Journal of Zoology 63:1773-1777.

Heulin, B., K. Osenegg-Leconte, and D. Michel. 1997. Demography of a bimodal reproductive species of lizard (*Lacerta vivipara*): Survival and density characteristics of oviparous populations. Herpetologica 53:432-444.

Heulin, B., K. Osenegg, and D. Michel. 1994. Survie et incubation des oeufs dans deux populations ovipares de *Lacerta vivipara*. Amphibia-Reptilia 15:199-219.

Hoffmann, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. Nature 470:479-485.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65-70.

Horváthová, T., C. Cooney, R., P. Fitze, S., T. Oksanen, A., D. Jelić, I. Ghira, T. Uller et al. 2013. Length of activity season drives geographic variation in body size of a widely distributed lizard. Ecology and Evolution 3:2424–2442.

Hulbert, A. J., and P. L. Else. 2004. Basal metabolic rate: history, composition, regulation, and usefulness.

Physiological and Biochemical Zoology 77:869-876.

IPCC. 2013. Summary for policymakers *in* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels et al., eds. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, NY, USA., Cambridge University Press.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455-1460.

—. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911-927.

Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution 50:434-437.

Le Galliard, J.-F., J. Cote, and P. S. Fitze. 2008. Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. Ecology 89:56-64.

Le Galliard, J.-F., P. S. Fitze, J. Cote, M. Massot, and J. Clobert. 2005b. Female common lizards (*Lacerta vivipara*) do not adjust their sex-biased investment in relation to the adult sex ratio. Journal of Evolutionary Biology 18:1455–1463.

Le Galliard, J.-F., P. S. Fitze, R. Ferrière, and J. Clobert. 2005c. Sex ratio bias, male aggression, and population collapse in lizards. Proceedings of the National Academy of Sciences of the United States of America 102:18231–18236.

Le Galliard, J.-F., O. Marquis, and M. Massot. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. Journal of Animal Ecology 79:1296-1307.

Le Galliard, J.-F., M. Massot, M. M. Landys, S. Meylan, and J. Clobert. 2006. Ontogenic sources of variation in sexual size dimorphism in a viviparous lizard. Journal of Evolutionary Biology 19:690 -704.

Lecomte, J., J. Clobert, and M. Massot. 1992. Sex identification in juveniles of *Lacerta vivipara*. Amphibia-Reptilia 13:21-25.

Lecomte, J., J. Clobert, M. Massot, and R. Barbault. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. Ecoscience 1:300-310.

Leips, J., J. Travis, and F. H. Rodd. 2000. Genetic influences on experimental population dynamics of the least killifish. Ecological Monographs 70:289-309.

Lindstrom, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology & Evolution 14:343-348.

Lindström, J., and H. Kokko. 2002. Cohort effects and population dynamics. Ecology Letters 5:338-344.

Lorenzon, P., J. Clobert, and M. Massot. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. Evolution 55:392-404.

Lorenzon, P., J. Clobert, A. Oppliger, and H. John-Alder. 1999. Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). Oecologia 118:423-430.

Marquis, O., M. Massot, and J.-F. Le Galliard. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. Ecology 89:2575-2583.

Maślak, R., Ł. Paśko, J. Kusznierz, and M. Moska. 2010. Sex ratio in population of Lacerta vivipara (Jacquin, 1787) (Sauria, Lacertidae) in a lowland habitat of the vicinity of Wrocław, SW Poland. Zeszyty Naukowe Uniwersytetu Przyrodniczego we Wrocławiu - Biologia i Hodowla Zwierzat 60:97-106.

Massot, M., J. Clobert, L. Montes-Poloni, C. Haussy, J. Cubo, and S. Meylan. 2011. An integrative study of ageing in a wild population of common lizards. Functional Ecology 25:848-858.

Massot, M., J. Clobert, T. Pilorge, J. Lecomte, and R. Barbault. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. Ecology 73:1742-1756.

McKinnon, J. S., and M. E. R. Pierotti. 2010. Colour polymorphism and correlated characters: genetic mechanisms and evolution. Molecular Ecology 19:5101-5125.

McLean, C. A., and D. Stuart-Fox. 2014. Geographic variation in animal colour polymorphisms and its role in speciation. Biological reviews of the Cambridge Philosophical Society 89:860-873.

McMahon, S. M., S. P. Harrison, W. S. Armbruster, P. J. Bartlein, C. M. Beale, M. E. Edwards, J. Kattge et al. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. Trends in Ecology & Evolution 26:249-259.

Melbourne, B. A., and A. Hastings. 2008. Extinction risk depends strongly on factors contributing to stochasticity. Nature 454:100-103.

Milá, B., Y. Surget-Groba, B. Heulin, A. Gosa, and P. S. Fitze. 2013. Multilocus phylogeography of the common lizard *Zootoca vivipara* at the Ibero-Pyrenean suture zone reveals lowland barriers and high-elevation introgression. BMC Evolutionary Biology 13:192.

Mousseau, T. A., and C. W. Fox. 1998. The adaptive significance of maternal effects. Trends in Ecology & Evolution 13:403-407.

Mugabo, M., O. Marquis, S. Perret, and J.-F. Le Galliard. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. Journal of Evolutionary Biology 23:1886 - 1898.

—. 2011. Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. Oecologia.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Australian Journal of Zoology 2:9-65.

Nokelainen, O., C. Lindstedt, and J. Mappes. 2013. Environment-mediated morph-linked immune and life-history

responses in the aposematic wood tiger moth. Journal of Animal Ecology 82:653-662.

Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R. Scheffers et al. 2015. Assessing species vulnerability to climate change. Nature Climate Change 5:215-224.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change, Pages 637-669 Annual Review of Ecology Evolution and Systematics.

Peñalver-Alcázar, M., P. Aragón, M. C. Breedveld, and P. S. Fitze. 2016. Microhabitat selection in the common lizard: implications of biotic interactions, age, sex, local processes and model transferability among populations. Ecology and Evolution.

Pertoldi, C., R. Bijlsma, and V. Loeschcke. 2007. Conservation genetics in a globally changing environment: present problems, paradoxes and future challenges. Biodiversity and Conservation 16:4147-4163.

Pilorge, T. 1987. Density size, structure, and reproductive characteristics of 3 populations of *Lacerta vivipara* (Sauria, Lacertidae). Herpetologica 43:345-356.

Pilorge, T., J. Clobert, M. Massot, J. J. van Gelder, H. Strijbosch, and P. J. M. Bergers. 1987. Life history variations according to sex and age in *Lacerta vivipara*, Pages 311-315 Proceedings of the 4th Ordinary General Meeting of the Societas Europaea Herpetologica., Societas Europaea Herpetologica, Faculty of Sciences, Nijmegen.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and t. R. D. C. Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-108.

Roig, J. M., M. A. Carretero, and G. A. Llorente. 2000. Reproductive cycle in a Pyrenean oviparous population of the common lizard (*Zootoca vivipara*). Netherlands Journal of Zoology 50:15-27.

San-Jose, L. M., F. Granado-Lorencio, and P. S. Fitze. 2012. Dietary lipids reduce the expression of carotenoid-based coloration in *Lacerta vivipara*. Functional Ecology 26:646–656.

San-Jose, L. M., F. Granado-Lorencio, B. Sinervo, and P. S. Fitze. 2013. Iridophores and not carotenoids account for chromatic variation of carotenoid-based coloration in common lizards (*Lacerta vivipara*). American Naturalist 181:396-409.

San-Jose, L. M., M. Peñalver-Alcázar, K. Huyghe, M. C. Breedveld, and P. S. Fitze. 2016. Inter-class competition in stage-structured populations: effects of adult density on life-history traits of adult and juvenile common lizards. Oecologia 182:1063-1074.

San-Jose, L. M., M. Peñalver-Alcázar, B. Milá, V. Gonzalez-Jimena, and P. S. Fitze. 2014. Cumulative frequency-dependent selective episodes allow for rapid morph cycles and rock-paper-scissors dynamics in species with overlapping generations. Proceedings of the Royal Society B: Biological Sciences 281:20140976.

Sgrò, C. M., A. J. Lowe, and A. A. Hoffmann. 2011. Building evolutionary resilience for conserving

biodiversity under climate change. Evolutionary Applications 4:326-337.

Sinclair, S. J., M. D. White, and G. R. Newell. 2010. How useful are species distribution models for managing biodiversity under future climates? Ecology and Society 15:8.

Sinervo, B., J. Clobert, D. B. Miles, A. McAdam, and L. T. Lancaster. 2008. The role of pleiotropy vs signaller-receiver gene epistasis in life history trade-offs: dissecting the genomic architecture of organismal design in social systems. Heredity 101:197-211.

Sinervo, B., B. Heulin, Y. Surget-Groba, J. Clobert, D. B. Miles, A. Corl, A. Chaine et al. 2007. Models of density-dependent genic selection and a new rock-paper-scissors social system. American Naturalist 170:663–680.

Sorci, G., J. Clobert, and S. Belichon. 1996a. Phenotypic plasticity of growth and survival in the common lizard *Lacerta vivipara*. Journal of Animal Ecology 65:781-790.

Stearns, S. C. 1992, The evolution of life histories. Oxford, UK, Oxford University Press.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275:649-659.

Wellenreuther, M., E. I. Svensson, and B. Hansson. 2014. Sexual selection and genetic colour polymorphisms in animals. Molecular Ecology 23:5398-5414.

Whiteley, A. R., S. W. Fitzpatrick, W. C. Funk, and D. A. Tallmon. 2015. Genetic rescue to the rescue. Trends in Ecology & Evolution 30:42-49.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009, Mixed effects models and extensions in ecology with R. New York, NY, USA, Springer.

SUPPLEMENTARY MATERIAL

Figure S2.1

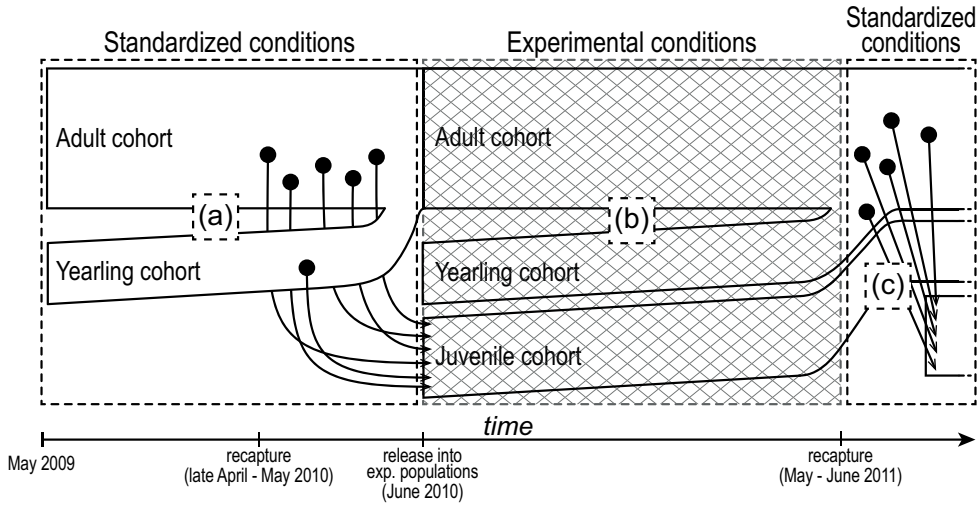


Figure S2.1: Experimental timeline. Initially, all lizards were maintained in enclosures under standardized conditions (a). Once gestation was advanced (i.e., late April - early May), all lizards were recaptured and maintained in the laboratory under standardized conditions. Adults and yearlings were released on the same day into enclosures with different humidity regimes and three different male color morph frequencies were established (cross-hatched part; b; Figure S2.2). The laid clutches of gravid females (full circles) were incubated under standardized conditions and newborn offspring released into experimental conditions the day after hatching (a; arrows). One year later, all individuals were recaptured, maintained in the laboratory, and laid clutches were again maintained under standardized conditions, in order to measure transgenerational treatment effects on phenotypic traits of newborn offspring (c). See also methods.

Figure S2.2

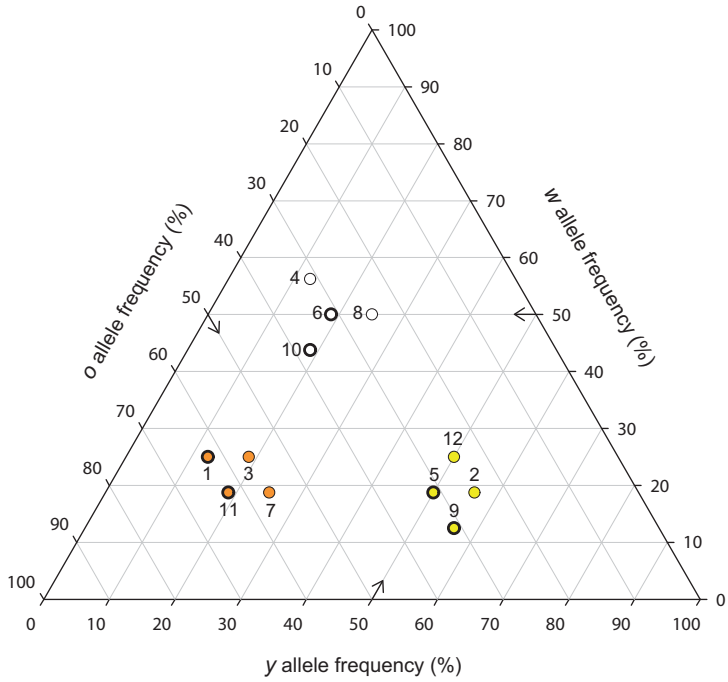


Figure S2.2: Ternary plot showing the initial (June 2010) adult male color morph frequency (CMF) of the 12 experimental populations. Three CMFs were established (Ob, Yb and Wb), each in four enclosures. In Ob, CMF was biased towards orange (*o*) allele dominance, in Yb towards yellow (*y*) allele dominance and in Wb towards white (*w*) allele dominance. Half of the populations of each CMF treatment were maintained under high humidity conditions (H; bold circle) and half under low humidity conditions (L; thin circle). In each population, 20 adults (8 males and 12 females), 5 to 6 yearlings (2 males and 3 or 4 females), and 18 to 20 newborn juveniles were released (population size: 43-46). Black arrows indicate the reading direction for each axis.

Figure S2.3

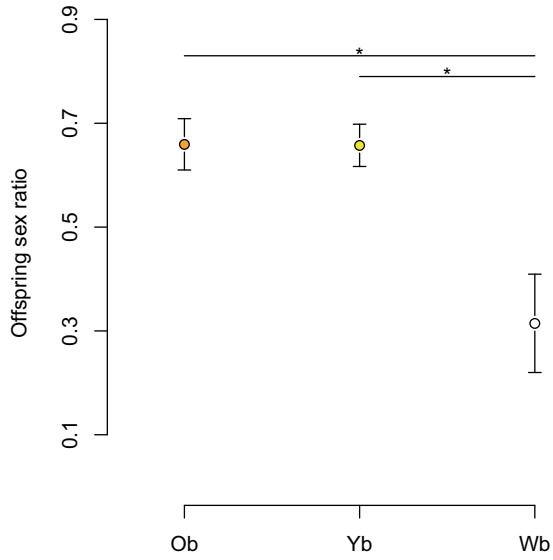


Figure S2.3: Color morph frequency (CMF) effects on offspring sex ratio (*n* male offspring/(*n* male offspring + *n* female offspring)). Data are given as mean ± SE. Horizontal bars depict *post hoc* contrasts and asterisks indicate statistical significance: * $P < 0.05$.

Figure S2.4

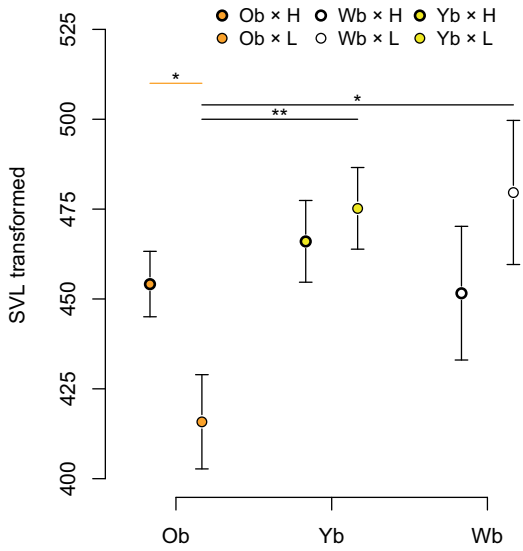


Figure S2.4: Effects of color morph frequency (CMF) and humidity treatment (H: High; L: Low) on SVL (mm) at hatching. Means ± SE are given. Horizontal bars depict *post hoc* contrasts and asterisks indicate statistical significance: * $P < 0.05$; ** $P < 0.01$.

Table 2.1: Treatment effects on juvenile, yearling, and adult final SVL (mm). Results of likelihood ratio tests are shown and the minimal adequate model is depicted in bold. Plain values correspond to the values before backward elimination.

Effects	Juveniles			Yearlings			Adults		
	χ^2	*df*	*P*	χ^2	*df*	*P*	χ^2	*df*	*P*
Fixed									
CMF	5.01	2	0.082	0.29	2	0.866	4.21	1	0.122
Humidity	1.07	1	0.301	**22.58**	**1**	**<0.001**	0.20	1	0.652
CMF × humidity	2.92	2	0.233	4.63	2	0.100	1.79	1	0.409
Sex	0.08	1	0.778	**79.83**	**1**	**<0.001**	**28.90**	**1**	**<0.001**
CMF × sex	†	†	†	2.61	2	0.271	1.24	1	0.539
Humidity × sex	0.14	1	0.703	**8.46**	**1**	**0.004**	1.76	1	0.185
ISVL (mm)	**6.05**	**1**	**0.014**	**24.23**	**1**	**<0.001**	**57.97**	**1**	**<0.001**
Time (days)	**11.11**	**1**	**<0.001**	1.43	1	0.232	0.936	1	0.333
Random									
Enclosure ID	**0.61**	**2**	**0.367**	**<0.01**	**2**	**0.500**	**<0.01**	**2**	**0.500**
Mother ID[Enclos. ID]	**<0.01**	**1**	**0.500**						

† not possible to model since not enough juveniles survived in each of the combinations.

Table S2.2: Treatment effects on juvenile growth rate (mm day^{-1}) for all time periods. Shown are likelihood ratio tests and *P* values of the minimum adequate model. Significant values are depicted in bold.

Effects	χ^2	*df*	*P*
Fixed			
CMF	**27.736**	**2**	**< 0.001**
Humidity	**12.221**	**1**	**< 0.001**
CMF × humidity	**10.544**	**2**	**0.005**
Sex	**5.161**	**1**	**0.023**
Hatching date (days)	**80.020**	**1**	**< 0.001**
Time period	**16.385**	**2**	**< 0.001**
Time period × sex	**7.547**	**2**	**0.023**
Time period × CMF	**51.758**	**4**	**< 0.001**
Time period × humidity	**11.180**	**2**	**0.004**
Time period × hatching date	**46.112**	**2**	**< 0.001**
Time period × CMF× humidity	**16.649**	**4**	**0.002**
Random			
Enclosure ID	0.420	2	0.405
Mother ID[Enclosure ID]	< 0.001	1	1.000

Table S2.3: Treatment effects on yearling growth rate (mm day^{-1}) for all time periods. Shown are likelihood ratio tests and *P* values of the minimum adequate model. Significant values are depicted in bold.

Effects	χ^2	*df*	*P*
Fixed			
CMF	**7.481**	**2**	**0.024**
Humidity	0.330	1	0.566
CMF × humidity	**9.690**	**2**	**0.008**
Sex	**6.584**	**1**	**0.010**
CMF × sex	2.732	2	0.255
Humidity × sex	2.559	1	0.110
ISVL (mm)	**8.257**	**1**	**< 0.001**
Time period	**59.922**	**2**	**< 0.001**
Time period × sex	**7.678**	**2**	**0.021**
Time period × CMF	**9.762**	**4**	**0.045**
Time period × humidity	5.648	2	0.059
Time period × ISVL	**13.377**		**0.001**
Time period × CMF × sex	**14.036**	**4**	**0.007**
Time period × CMF × humidity	**11.599**	**4**	**0.021**
Time period × humidity × sex	**7.953**	**2**	**0.019**
Time period × humidity × ISVL	**6.448**	**2**	**0.040**
Random			
Enclosure ID	< 0.001	2	0.500

Table S2.4: Indirect treatment effects on offspring traits: Offspring SVL (mm), tail length (mm) and body condition at hatching. In the analysis on body condition, offspring tail length was additionally included as a covariate. Results of likelihood ratio tests are shown and the minimal adequate model is depicted in bold. Plain values correspond to the values before backward elimination.

Effects	SVL			Tail length			Body condition		
	χ^2	*df*	*P*	χ^2	*df*	*P*	χ^2	*df*	*P*
Fixed									
CMF	**0.94**	**2**	**0.625**	0.56	2	0.757	0.32	2	0.852
Humidity	**6.77**	**1**	**0.009**	0.26	1	0.608	0.13	1	0.718
CMF × humidity	**7.51**	**2**	**0.023**	0.42	2	0.811	0.36	2	0.834
Sex	**45.75**	**1**	**< 0.001**	**13.94**	**1**	**< 0.001**	**27.28**	**1**	**< 0.001**
CMF × sex	3.31	2	0.191	3.45	2	0.178	1.46	2	0.482
Humidity × sex	0.36	1	0.549	0.05	1	0.817	0.53	1	0.466
Relative clutch size	**11.86**	**1**	**< 0.001**	2.56	1	0.110	0.05	1	0.814
Hatching date (days)	**12.73**	**1**	**< 0.001**	1.94	1	0.164	0.05	1	0.829
Tail length (mm)							**43.72**		**< 0.001**
Random									
Enclosure ID	**0.51**	**2**	**0.387**	**3.24**	**2**	**0.099**	**0.034**	**2**	**0.491**
Mother ID[Enclos. ID]	**44.46**	**1**	**< 0.001**	**79.37**	**1**	**< 0.001**	**30.57**	**1**	**< 0.001**

Table S2.5: Treatment effects on yearling body condition change (i.e., difference in BC between two captures divided by the number of days passed) for all time periods. Shown are likelihood ratio tests and *P* values of the minimum adequate model. Significant values are depicted in bold.

Effects	χ^2	*df*	*P*
Fixed			
CMF	2.833	2	0.242
Humidity	1.232	1	0.267
CMF × humidity	**6.463**	**2**	**0.039**
Sex	**4.138**	**1**	**0.042**
CMF × sex	1.106	2	0.575
Humidity × sex	**5.841**	**1**	**0.016**
IBC	**6.353**	**1**	**0.012**
Time period	**8.505**	**2**	**0.014**
Time period × sex	**11.041**	**2**	**0.004**
Time period × IBC	**9.029**	**2**	**0.011**
Time period × CMF	**19.533**	**4**	**< 0.001**
Time period × humidity	**12.791**	**2**	**0.002**
Time period × CMF × sex	**12.743**	**4**	**0.013**
Time period × humidity × sex	**10.509**	**2**	**0.005**
Time period × CMF × humidity	**26.725**	**4**	**< 0.001**
Random			
Enclosure ID	<0.001	2	0.500

Appendix A. Results: Treatment effects by time period

1. Humidity × CMF effects on juvenile growth

There was a significant triple interaction between humidity treatment, CMF treatment, and time period on juvenile growth rate rate (χ^2_4 = 16.65, P = 0.002, Table S2.2; Figure 2.2*a*). *Post hoc* tests on growth rate between release and August revealed significantly higher growth rates in Ob and Yb populations of L compared to H humidity (χ^2_1 = 16.83, P < 0.001; χ^2_1 = 18.98, P < 0.001, respectively; Figure 2.2*a*) and in Wb populations growth rates tended to be higher in H compared to L humidity (χ^2_1 = 3.00, P = 0.083). In H humidity, juveniles of Yb populations exhibited lower growth rates than those of Ob and Wb populations (χ^2_1 = 16.28, P < 0.001; χ^2_1 = 10.41, P = 0.004, respectively). In L humidity, juveniles of Ob populations exhibited higher growth rates than those of Yb and Wb populations (χ^2_1 = 10.86, P = 0.004; χ^2_1 = 26.79, P < 0.001, respectively). Growth rates between August and September significantly differed between humidity groups, with L juveniles growing 0.045 ± 0.013 mm day^{-1} faster than H humidity juveniles (Table 2.2). CMF tended to affect growth rate (P = 0.055) and no significant interaction between CMF and humidity existed (Table 2.2). Juvenile growth from September to June was significantly affected by an interaction between CMF and humidity. In the Yb treatment, juveniles in H humidity grew significantly faster than in L (χ^2_1 = 17.12, P < 0.001; Figure 2.2*a*), and there were no significant differences in the Wb and Ob populations (P = 1.000). In H humidity, juveniles of Yb populations grew significantly faster than those of Ob and Wb populations (χ^2_1 = 14.71, P < 0.001; χ^2_1 = 7.94, P = 0.024, respectively). In L humidity, no significant differences existed between CMF treatment groups (all P > 0.050). Differences in growth rate from release to August were thus compensated by differences in growth from September to June (e.g., in H, lower growth rate of Yb from release to August was compensated by higher growth rate of Yb from September to June), resulting in no interactive effect on Final SVL.

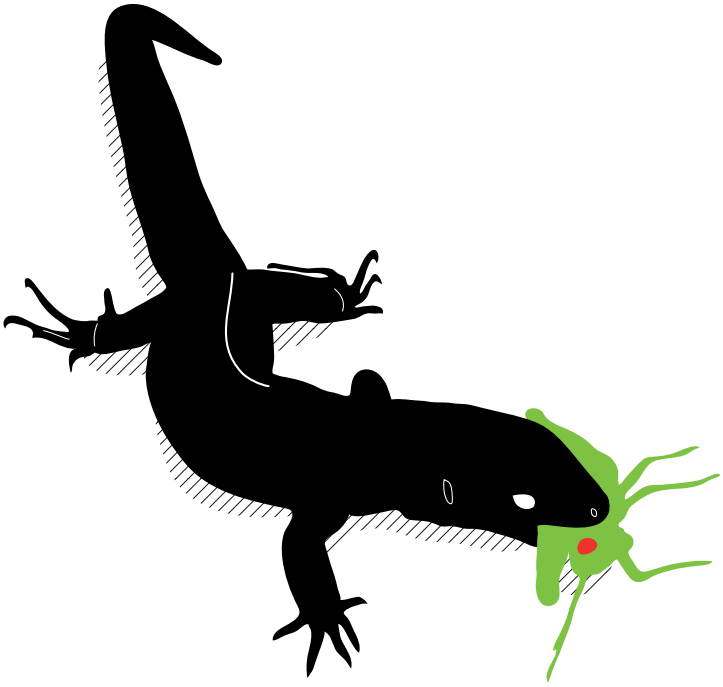
2. CMF × sex effects on yearling growth

There was a significant interaction between CMF, sex and time period on yearling growth rate (Table S2.3). Rerunning the model with Yb and Wb populations only (excluding Ob populations) rendered a significant interaction between CMF, sex and time period (χ^2_2 = 11.52, P = 0.003), while rerunning the model with Yb and Ob populations only (excluding Wb populations) rendered no significant interaction (χ^2_2 =

3.76, $P = 0.153$). This shows that the interaction arose due to the opposite growth patterns existing in Yb and Wb populations. In Yb populations females grew faster in both time periods (Figure 2.2*c*) and in Wb populations females grew faster than males from release to August, while males grew faster than females from August to September (Figure 2.2*c*). In Wb populations, differential growth between sexes from release to August was compensated by differential growth between sexes from August to September, leading to no significant CMF × sex interaction on Final SVL (Table S2.1).

Chapter II

Climatic stochasticity and age-specific effects on life-histories of structured populations of common lizards



Cristina Romero-Diaz & Patrick S. Fitze

ABSTRACT

Climatic stochasticity can affect population dynamics through changes in individual life-history traits via two routes: directly affecting demographic rates and/or indirectly through changes in population density. In structured populations, life-history traits may be affected in a stage-specific manner and increased stochasticity could disrupt population structure, leading to long-term population decline. Increased climatic stochasticity, including increased frequency of climatic extremes, is one of the main predictions of climate change and thus it is crucial to understand how life-history components respond to abiotic fluctuations. We experimentally manipulated precipitation stochasticity and the occurrence of extreme events in age-structured populations of a short-lived ectothermic vertebrate and assessed individual growth, survival and reproductive success during one year. Increased stochasticity led to reduced annual survival probability in all age classes of the population. Asymmetric contest competition and inter-cohort agonistic social interactions were likely the mechanisms involved. The effects of extreme events usually depended on the level of stochasticity or individual features (e.g., sex). The probability of reproducing differed with age, but not among treatments. However, overall reproductive output was higher in lightly stochastic populations and females exhibited alternative strategies with respect to reproductive timing and investment under different stochasticity levels, with potential adaptive value. We discuss the potential consequences of increased climatic stochasticity on population structure and growth.

Keywords: Population dynamics, age-structured populations, *Zootoca vivipara*, climate change, humidity, extremes.

Individual life-history phenotypes result from complex interactions between gene expression and environmental conditions during ontogeny (West-Eberhard 2003). The biotic (e.g., food resources) and abiotic (e.g., climate) environment commonly experience stochastic variation over time and/or space and environmental stochasticity can strongly affect population dynamics through changes in life-history traits (Benton and Beckerman 2005; Koons et al. 2008; Sæther 1997; Steiner et al. 2014).

In structured populations, where individuals are classified into different stages according to, e.g., age, size or ontogenetic development, life-history traits of certain age or stage classes may be much more susceptible to stochastic perturbation than others (Benton et al. 2006), i.e., individual reproductive rates or timing and survival in response to stochasticity can vary with stage and age (Steiner et al. 2014). When life-history traits are affected in a stage-specific manner, this increases the complexity of the effects of environmental stochasticity,

which makes them harder to predict. Unfortunately, theoretical population models often ignore stochasticity and simplify populations' structure, albeit every natural environment fluctuates to some degree and most animal populations have complex stage-structures.

Environmental stochasticity may influence population dynamics in two ways: First, through direct effects on demographic parameters (e.g., size and structure) of the current population; and second, as a consequence of interactive effects with density-dependence (Benton and Beckerman 2005; Coulson and Godfray 2007). For example, weather stochasticity can have direct effects on life-history traits, e.g., stage-dependent growth, survival, and reproduction, which are linked to population growth rate (Coulson et al. 2006; Dublin and Lotka 1925; Steiner et al. 2014) and thus population size. In turn, population size (density) affects the intensity of competition, predation, parasitism, or disease among individuals (Anderson and May 1978; Samhouri et al. 2009) and can modify the future trajectory of the population.

In structured populations, the disruption of population structure by changes in individual life-histories increases the variance in annual population growth rate, which tends to reduce population growth rates on the long-term (Coulson and Godfray 2007; Drake 2005; Saltz et al. 2006). Furthermore, a positive temporal correlation between stochastic effects frequently occurs, potentially increasing their severity (Johst and Wissel 1997; Marion et al. 2000). All of the above leads to a higher probability of population extinction (Coulson and Godfray 2007; Lande 1993) and thus uncovering whether and by which underlying mechanisms environmental stochasticity affects life-histories of individuals in structured populations is of central interest.

One of the most relevant sources of environmental stochasticity is climate and, consequently, climate change. Therefore, it is crucial to identify how and through which life-history components climatic variables affect demographic rates of populations (Boyce et al. 2006; Hallett et al. 2004). This will allow understanding species' vulnerability to climate change, especially since life-history traits are good determinants of population dynamics and extinction probability (Dawson et al. 2011; Jiguet et al. 2007; Pacifici et al. 2015). To this end, the limiting factors leading to population decline and extinction need to be identified and experimentally validated (Caughley 1994). However, very few experiments have manipulated candidate

limiting factors and thus the proximate causes of climate-related extinctions remain obscure (Boyce et al. 2006; Cahill et al. 2013).

Model projections on future climate change (IPCC 2013) agree that by the end of the 21st century an increase in the intensity and frequency of extreme events (e.g., more frequent hot temperature extremes, more frequent and intense extreme precipitation events, longer and frequent heat waves) and precipitation variability on regional scales will be very likely. In sum, climate change is expected to alter environmental variability, increasing climatic stochasticity (Boyce et al. 2006; Easterling et al. 2000), which may increase population extinction risk (see above). Climate extremes could be an important component of stochasticity; they are involved in shaping species distributions (Kerr and Kharouba 2007), have been shown to drive local population dynamics in some taxa (e.g., butterflies, birds; Parmesan et al. 2000), and are associated with population extinction events (Ehrlich et al. 1980; Thomas et al. 1996). Yet the understanding of the relationships between climatic stochasticity, extreme events and the biotic processes that determine population dynamics is limited.

The aim of the current study was to provide the first robust experimental evidence unraveling whether climatic stochasticity might be an important source of population decline and extinction. The effects of stochasticity were assessed on individual life-history traits in structured populations, allowing us to identify the biological mechanisms through which life-history traits may modify complex intra-population dynamics. Climatic stochasticity was manipulated in two ways: through the stochasticity of precipitation and the occurrence of extreme events. The independent and simultaneous manipulation of these two factors that under natural conditions are predicted to coincide further allowed pinpointing the effects' origin.

We used an ectothermic species, the Eurasian common lizard (*Zootoca vivipara*), as model organism since reptiles are particularly threatened by climate change due to their generally reduced dispersal capacity and high dependence on local climatic conditions (Araújo et al. 2011; Araújo et al. 2006). Under available climatic scenarios for the 21st century, the potential distribution area of most species of reptiles in Europe (including *Z. vivipara*) is predicted to contract (Araújo et al. 2011; Araújo et al. 2006). *Z. vivipara* is the lacertid with the world's largest geographical distribution. It inhabits hygrophilic environments and its geographic distribution is limited by

humidity conditions (Ceiran 2007), especially in southern populations. Its water requirements are associated with growth and activity patterns (Grenot et al. 1987; Lorenzon et al. 1999; chapter I). affecting survival and reproduction (Lorenzon et al. 2001) and thus potentially population dynamics.

Here, we predicted negative effects of increased stochasticity on individual life-history traits, particularly of the youngest age classes, resulting in short- (and potentially long-) term population decline. Growth rates, survival, or reproductive success may be negatively affected due to energetic constraints derived from disturbed resource availability (i.e., reduced carrying capacity) and/or increased intra-population competition (Mugabo et al. 2011; Mugabo et al. 2010). Changes on survival probability are expected to have a more immediate effect on population size than changes in growth patterns or reproductive investment, which allow for compensatory responses later in life (Bleu et al. 2013; Le Galliard et al. 2008; Le Galliard et al. 2010). The timing of reproduction was also predicted to be affected by climatic stochasticity, in line with previously documented changes in the phenology of many taxa in response to climate change (Parmesan 2006). We predicted predominantly short-term effects of extreme events, proportional to the relative magnitude of the simulated event, presumably through similar biological mechanisms (Parmesan et al. 2000).

MATERIALS AND METHODS

Study species

Populations of *Z. vivipara* are stage-structured, sexually dimorphic (Braña 1996) and exhibit overlapping generations. For individuals that survive to their first birthday average lifespan is 4 - 5 years, and despite growth being continuous throughout life, in general the species' ontogenetic development can be divided into three distinct age classes—namely juveniles (newborn individuals), yearlings (born the previous season), and adults—based on differences in body size and coloration (Avery 1975a; Bauwens and Verheyen 1985; Pilorge and Castanet 1981). Mortality is highest in juveniles (up to 90%; Adolph and Porter 1993; Avery 1975a; Heulin et al. 1997; Pilorge and Castanet 1981) and conditions experienced during early development importantly affect immediate and subsequent performance (e.g., Massot and Aragon 2013; Mugabo et al. 2010). Age at maturation is size-dependent and is determined by growth during the first year of life (Heulin 1985b). Growth and survival determine the recruitment rate in the population. In our study system, males start to emerge from hibernation at

the end of February-early March, followed by females a few weeks later. The mating period starts immediately after female emergence (Breedveld and Fitze 2015). In the Pyrenean populations, *Z. vivipara* is oviparous and average clutch size is 5 eggs (Peñalver-Alcázar et al. 2015). Female snout-to-vent-length (SVL) and clutch size are positively correlated (Avery 1975b).

Experimental design

All lizards used for this experiment originated from natural populations of the Spanish central Pyrenees ("NE Spain" clade, Milá et al. 2013). In June 2011, we established 12 independent, semi-natural lizard populations at el Boalar, Jaca (Huesca, Spain), located within 75km distance from *Z. vivipara*'s natural distribution area. Each population was enclosed by galvanized metal walls and covered by a net, preventing escapes and terrestrial or avian predation. Enclosures consisted of 100 m^2 of planted vegetation, two water ponds, 14 logs, and four stone piles, providing natural food, water, basking sites and shelters. All populations comprised 20 adults (males n = 8, females n = 12), 5 to 7 yearlings (males n = 2 - 4, females n = 2 - 4) and 25 to 30 newborn juveniles (51 - 56 individuals per population in total). Lizards were individually marked by toe-clipping, weighted (± 1 mg) and measured (± 1 mm) before release. At release, there were no significant differences in SVL and body condition (i.e., the residuals from the regression between SVL and body mass) among populations in any of the age classes (SVL: Adults: $F_{11,228}$ = 0.31, P = 0.98; yearlings: $F_{11,59}$ = 0.36, P = 0.97; juveniles: $F_{11,319}$ = 0.29, P = 0.987; BC: Adults: $F_{11,228}$ = 0.29, P = 0.987; yearlings: $F_{11,59}$ = 0.40, P = 0.950; juveniles: $F_{11,319}$ = 1.11, P = 0.354).

Two experimental treatments, each taking two levels, were applied at the population level using a 2 x 2 factorial design. Each treatment combination thus consisted of three enclosures. Firstly, climatic stochasticity was manipulated by simulating differences in precipitation using two alternative sprinkling regimes: highly stochastic ("HS"), when the sprinkling frequency was random, or lightly stochastic ("LS"), when the sprinkling frequency was regular. Each treatment level was assigned to six populations. LS populations were sprinkled twice a day, at 9.00 a.m. and 6.00 p.m. for 5 minutes, i.e., 28 times per fortnight. HS populations were also sprinkled 28 times per fortnight (for 5 minutes each) but at randomized hours and days. Secondly, in half of the populations extreme events ("E") were simulated, while in the other half no extreme ("nE") events existed. Extreme weather events are defined as weather events that rarely occur at a particular

place and time of year (extreme frequency), or have very severe magnitude (extreme intensity). Statistically, an event of extreme frequency or intensity lies in the upper or lower 10th percentile of the probability distribution of observations (IPCC 2014a). The simulated extreme events occurred once per month (June, July, August, and September) and consisted of 1 hour of uninterrupted water sprinkling. The average intensity of produced precipitation was ≥ 15 mm/h, which corresponds to the lower limit of "intense" intensity of precipitation according to the Spanish State Meteorological Agency (AEMET; intense precipitation: > 15 ≤ 30 mm/h). Events of "intense" (and above) intensity of precipitation are naturally rare during the summer months and occur with an average frequency of ≤ 0.75 times per month, according to daily observational precipitation data recorded in the region for 59 years (Table S3.1). In LS populations, extreme events happened on the 15th of each month, whereas in HS populations extreme events occurred at a random day of the month. To manipulate the stochasticity of the supplied water, but not the amount of supplied water *per se*, the duration of daily sprinkling was adjusted in E populations by subtracting 1 minute of sprinkling per sprinkling event, so that every 30 days the total amount of water supplied to every treatment group (and population) was the same.

Growth and annual survival measurements

After the initial release, individuals were recaptured in August and September using a robust design with three successive secondary sampling days per primary capture session. In June of the following year, all alive lizards were recaptured by emptying the enclosures. SVL (to the nearest mm) and body mass (to the nearest mg) of all captured individuals were measured. Growth rates were estimated as the difference in SVL between two captures divided by the interval of time passed (ΔSVL/ΔTime). The growth rate estimate between September and June excluded the time spent in hibernation (assumed to be from the 1st of November to the 1st of March (e.g., chapter I). SVL at the recapture in June was termed "final SVL". Recapture probability in June was 1, thus annual survival probability was directly derived from the recapture data.

Reproduction

During the breeding season, females were regularly captured and the developmental status of the eggs verified using abdominal palpation. Females in an early stage of pregnancy were released at the capture location, while those in an advanced stage of pregnancy were

brought into the laboratory and housed in individual *terraria* until egg laying. *Terraria* (20 x 15 x 15 cm) contained 2 cm of peat soil substrate, a shelter, a water pool and a basking surface, and were maintained at a light cycle of 12L:12D. UV light was provided for two hours a day (from 12 a.m. to 2 p.m.) to facilitate calcium metabolism. Water was available *ad libitum* and food items were provided every other day (*larvae* of *Galleria mellonella*, *Acheta domestica*, or *Lumbricus terrestris*). Once a week, diet was complemented with a standard reptile supplement of calcium (Microcalcium TerraVit, JBL, Neuhofen, Germany). Inspection for laid clutches was performed daily in the morning and late in the afternoon. For detected clutches, laying date, clutch size (number of eggs), clutch weight and female weight were recorded. Laid clutches were incubated at 21°C during the day and 19°C during the night (Heulin et al. 1994) in standard refrigerated incubators with a humid environment. Hatching date was noted and incubation time calculated (i.e., number of days passed between laying and hatching) for every hatchling.

Statistics

Statistical analyses were performed in R version 2.15.2. Growth rates, final SVL and annual survival were analyzed separately for each age class with mixed-effects models using package nlme (Pinheiro et al. 2013) for Gaussian distributions and lme4 (Bates et al. 2013) for non-Gaussian (poisson or binomial) distributions. Treatments—stochasticity and extreme events—and sex were modeled as fixed factors, and whenever possible their first and second order interactions were included in the model. Initial body size (ISVL; i.e., SVL at hatching for juveniles and SVL at release for yearlings and adults) was modeled as a covariate. Enclosure identity was modeled as a random effect. Juvenile analyses additionally included hatching date as a covariate in the models on growth and survival, and clutch identity nested within enclosure identity, modeled as a random effect. Models analyzing final SVL included total time spent in the enclosures for all age classes.

The probability of a surviving female being gravid (gravid = 1 / non-gravid = 0) (e.g., Lorenzon et al. 2001) , clutch size, relative clutch size ("Rclsize"; the residuals of the regression between female SVL and clutch size—which is a size-independent measure of female reproductive effort), and laying date were analyzed for all females, and incubation time for all hatchlings. These models included treatments as fixed effects, female/mother age class (i.e., the age they were at release) and their interactions, as well as enclosure identity as a random factor. Clutch identity, nested within

enclosure identity was modeled as a random factor in the case of incubation time analysis. SVL was used instead of age class in clutch size analysis. Laying date was added as a covariate in clutch size and Rclsize analyses, and the latter as a covariate in laying date analysis. Hatchling size and Rclsize were included as covariates in incubation time analysis. Quadratic relationships between covariates and independent variables were tested and a significant effect existed only between Rclsize and incubation time.

Model simplification was performed following Zuur et al. (2009) and

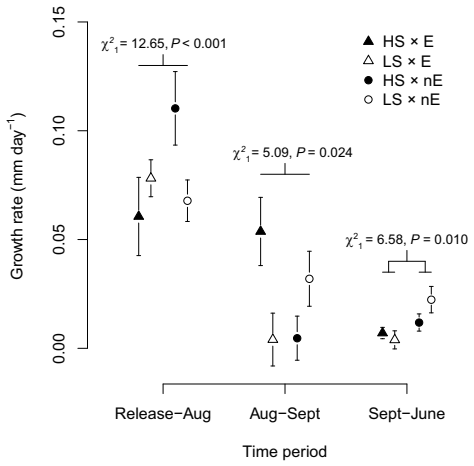


Figure 3.1 Treatment effects (stochasticity × extreme events) on yearling growth rate from release to August (n = 54), August to September (n = 34), and September to June (n = 28). Shown are means ± SE. Likelihood ratios (χ^2), degrees of freedom and P - values from the LMM are given. Horizontal lines indicate significant interactions, while tree-like lines indicate significant main effects, i.e. between extreme events treatment groups.

significance of model terms was assessed using likelihood ratio tests. Model assumptions of normality and homogeneity of variance were verified on the residuals. *Post hoc* tests were performed using Tukey tests or pairwise contrasts with a Holm-Bonferroni correction (Holm 1979). Significance levels of all reported tests are two-tailed with P = 0.05. P - values for random effects were corrected for testing on the boundary (Zuur et al. 2009). Estimates are always presented with standard errors.

RESULTS

Growth pattern

Juveniles

Final SVL was unaffected by the treatments (all P > 0.799), sex, ISVL, total time spent in the enclosure, and the interaction between sex and ISVL (all P > 0.151).

Stochasticity significantly affected juvenile growth rate from September to June. Juveniles grew 0.020 ± 0.006 mm day^{-1} faster in HS than in LS populations (n = 57; χ^2_1 = 7.18, P = 0.007). Extreme events was not significant (χ^2_1 = 0.01, P = 0.903) and none of the treatments affected juvenile growth rate in the other time periods (all P > 0.406). From release to August, juvenile growth rate was negatively correlated to hatching date (n =

126; χ^2_1 = 18.49, P < 0.001), and from September to June it was positively correlated (n = 57; χ^2_1 = 8.16, P = 0.004). Sex, ISVL and their interaction was not significant in any time period (all P > 0.223).

Yearlings

Yearling final SVL was not significantly affected by the treatments (P > 0.148) but it differed between sexes (n = 43; χ^2_1 = 16.26, P < 0.001; females SVL - male SVL: 3.29 ± 0.75 mm) and ISVL was positively correlated (χ^2_1 = 9.92, P = 0.001). Total time spent in the enclosure and the interaction between sex and ISVL were not significant (all P = 0.357).

Yearling growth rates were significantly affected by an interaction between stochasticity and extreme events from release to August and August to September (statistics in Figure 3.1). In both cases, there was a crossover interaction and while neither difference in means between the levels of one factor within a specific level of the other was significantly different from zero, they were significantly different from each other. From release to August, the difference between HS and LS (i.e., HS - LS) was negative in E populations and it was positive in nE populations (Figure 3.1). From August to September, the difference between HS and LS was positive in E populations and negative in nE populations (Figure 3.1). Yearling growth rate was also affected by an interaction between extreme events and sex from release to August (n = 54; χ^2_1 = 4.71, P = 0.030). *Post hoc* tests revealed that males in nE populations grew faster than males in E (χ^2_1 = 7.76, P = 0.011), and in E, females grew faster than males (χ^2_1 = 13.28, P < 0.001). From September to June, yearling growth rate was significantly affected by extreme events (Figure 3.1). Individuals of nE populations grew faster than those of E populations.

From August to September, there was a significant interaction between sex and ISVL (χ^2_1 = 7.48, P = 0.006). While growth rate was negatively correlated with ISVL in males (χ^2_1 = 6.10, P = 0.027), females were unaffected (χ^2_1 = 1.69, P = 0.193). Sex did not affect growth rate from September to June (P > 0.555). ISVL was negatively correlated with yearling growth rate from release to August (χ^2_1 = 30.92, P < 0.001), but not from September to June (P > 0.058).

Adults

Final SVL was significantly affected by stochasticity (n = 135; χ^2_1 = 4.02, P = 0.045). Lizards in LS populations grew 0.499 ± 0.251 mm larger than those in HS populations. Furthermore, final SVL differed between sexes (χ^2_1 = 23.08, P < 0.001); females were on average 1.541 ±

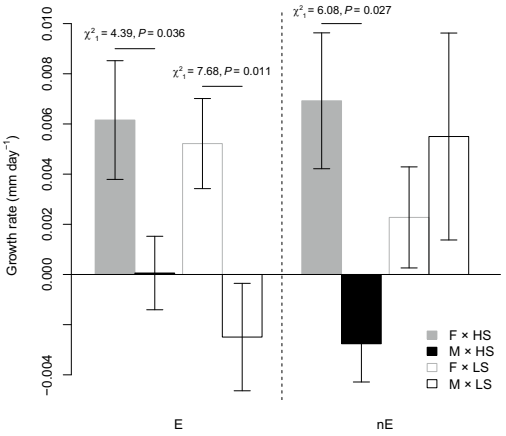


Figure 3.2 Treatment effects (stochasticity × extreme events × sex) on adult growth rate from September to June (n = 91). Shown are means ± SE. Likelihood ratios (χ^2), degrees of freedom and P - values from *post hoc* contrasts are given.

0.314 mm larger than males. Final SVL was positively correlated with ISVL (χ^2_1 = 150.97, P < 0.001) but unaffected by total time spent within the enclosure (χ^2_1 = 0.27, P = 0.600).

From September to June, adult growth rate was affected by a triple interaction among stochasticity, extreme events and sex (n = 91; χ^2_1 = 5.09, P = 0.024). Females grew faster than males in both extreme events treatment groups of HS populations and females also grew faster than males in LS, E populations (Figure 3.2).

From release to August, growth rate was significantly affected by stochasticity (n = 193; χ^2_1 = 4.17, P = 0.041) and not by extreme events (χ^2_1 = 0.07, P > 0.794). Adults grew faster in LS populations than in HS populations (estimate: 0.008 ± 0.004 mm day^{-1}). From August to September, growth rate was significantly affected by an interaction between stochasticity and sex (n = 139; χ^2_1 = 4.24, P = 0.039) and extreme events was not significant (χ^2_1 = 1.44, P > 0.231). *Post hoc* contrasts revealed that females grew faster in LS than HS populations (χ^2_1 = 9.10, P = 0.005), while males were unaffected (χ^2_1 = 0.02, P = 0.880). From release to August, females grew faster than males (χ^2_1 = 26.79, P < 0.001; estimate: 0.018 ± 0.003 mm day^{-1}) and growth rate was negatively correlated with ISVL (χ^2_1 = 48.02, P < 0.001). ISVL was not significant in the other time periods and the interaction between sex and ISVL was never significant (all P > 0.457).

Survival

Juveniles

Juvenile survival was affected by a significant interaction between stochasticity and sex (Table 3.1, Figure 3.3). While males exhibited higher survival in LS populations, females exhibited similar survival in LS and HS populations. Survival was negatively affected by hatching date (Table 1), i.e., juveniles born earlier in the season had higher survival probability.

Table 3.1 Treatment effects on annual survival of juveniles (n = 291), yearlings (n = 71) and adults (n = 238). The minimum adequate model is depicted in bold. Significance of model terms was tested using likelihood ratio tests (χ^2).

Effects	Juveniles			Yearlings			Adults		
	χ^2	*df*	*P*	χ^2	*df*	*P*	χ^2	*df*	*P*
Stochasticity	**0.01**	**1**	**0.936**	**6.37**	**1**	**0.011**	**4.61**	**1**	**0.032**
Extreme events (EE)	0.02	1	0.882	0.42	1	0.515	0.77	1	0.381
Stochasticity × EE	0.01	1	0.920	0.00	1	0.998	0.02	1	0.893
Sex	**1.78**	**1**	**0.182**	**0.19**	**1**	**0.664**	**10.05**	**1**	**0.001**
Stochasticity × sex	**4.70**	**1**	**0.030**	1.67	1	0.196	0.00	1	0.974
Extreme events × sex	0.03	1	0.862	0.04	1	0.848	1.26	1	0.262
ISVL (mm)	0.13	1	0.722	**7.10**	**1**	**0.007**	2.00	1	0.158
ISVL × sex	0.02	1	0.881	**5.98**	**1**	**0.014**	3.13	1	0.077
Hatching date (days)	**30.87**	**1**	**< 0.001**						

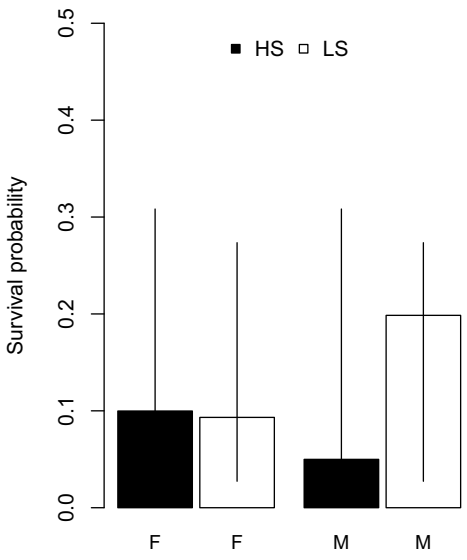


Figure 3.3 Annual survival of juveniles in relation to stochasticity treatment and sex. Shown are mean expected survival probabilities ± 95% CI. Sample size: n = 291.

Extreme events, ISVL and all other interactions were not significant.

Yearlings

Yearlings survived better in LS than HS populations (Table 3.1; estimate [logits]: 1.458 ± 0.570). Survival was also affected by an interaction between sex and ISVL (Table 3.1). ISVL was negatively correlated with survival in females (χ^2_1 = 7.10, P = 0.015), but not in males (χ^2_1 = 0.38, P = 0.535). Extreme events and all other interactions were not significant.

Adults

Adults survived significantly better in LS than HS populations (estimate [logits]:

1.213 ± 0.516; Table 3.1) and males exhibited higher survival than females (estimate [logits]: 0.955 ± 0.304; Table 3.1). Extreme events, ISVL and all interactions were not significant.

Reproductive success

Probability of being gravid

The probability of being gravid was not significantly affected by stochasticity and extreme events (χ^2_1 = 0.20, P = 0.656; χ^2_1 = 0.13, P = 0.722, respectively) and it depended on the female's age class (χ^2_2 = 98.96, P < 0.001). Adult and yearling females were significantly more likely of being gravid than juveniles (yearlings in June; *Post hoc*: Z = 7.33, P < 0.001; Z = 4.39, P < 0.001, respectively; predicted probabilities: adults: 0.90, 95% CI [0.80,0.95]; yearlings: 0.95, 95% CI [0.70,0.99]; juveniles: 0.11, 95% CI [0.05,0.24]). Minimum body size of gravid females was 50 mm and only 5 females born the previous year (i.e., released juveniles) were gravid (1 in HS, 4 in LS populations).

Age-specific reproductive investment and timing of reproduction

Females laid a total of 85 clutches among all populations: 34 clutches in HS versus 51 clutches in LS, and 41 in E versus 44 in nE.

Clutch size was unaffected by treatments, laying date and their interactions (all P > 0.347) and it was positively correlated with female SVL (n = 85; χ^2_1 = 7.68, P < 0.001). Body-size independent reproductive investment of females (Rclsize) significantly differed among stochasticity treatments (χ^2_1 = 11.69, P < 0.001). Rclsize was higher in HS than in LS populations (estimate: 0.740 ± 0.346). Moreover, Rclsize was significantly affected by an interaction between extreme events and laying date (n = 85; χ^2_1 = 6.44, P = 0.011). Rclsize was significantly lower in E compared to nE populations for laying dates above the mean (Figure 3.4). Additionally, Rclsize significantly differed among age classes (χ^2_2 = 7.68, P = 0.021). Yearling females exhibited significantly higher Rclsize than adult females (*Post hoc*: Z = 3.17, P =

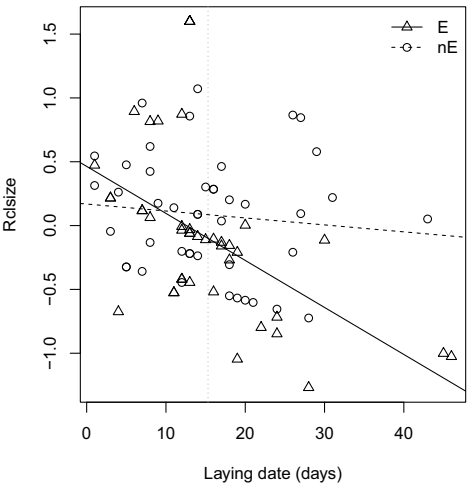


Figure 3.4 Effects of extreme events on relative clutch size (Rclsize) by laying date. Data points and lines are predicted from the LMM. The vertical dotted line depicts mean laying date (15.3 days).

0.004).

Laying date significantly differed between stochasticity treatments (n = 85; χ^2_1 = 6.39, P = 0.011); females in LS populations laid 4.04 ± 1.42 days later than females in HS. Laying date was age-specific, with adults and yearlings laying earlier than juveniles (χ^2_1 = 10.99, P = 0.004; *Post hoc*: Z = 6.47, P < 0.001; Z = 5.66, P < 0.001, respectively).

Incubation time was significantly affected by an interaction between stochasticity and the quadratic Rclsize (n = 195; χ^2_1 = 12.80, P = 0.002; Figure 3.5). In HS populations, incubation time increased with female investment, reached a maximum around Rclsize = 1 and thereafter decreased (χ^2_1 = 8.51, P = 0.007). In contrast, in LS populations incubation time did not depend on Rclsize (χ^2_1 = 2.72, P = 0.099). There existed a significant interaction between mother age class and hatchling size (χ^2_1 = 12.01, P = 0.002). *Post hoc* analyses revealed that the incubation time of the eggs laid by juveniles (current yearlings) had a negative correlation with hatchling size (χ^2_1 = 37.74, P < 0.001), while this effect was non-significant in females of other age classes (all P > 0.290).

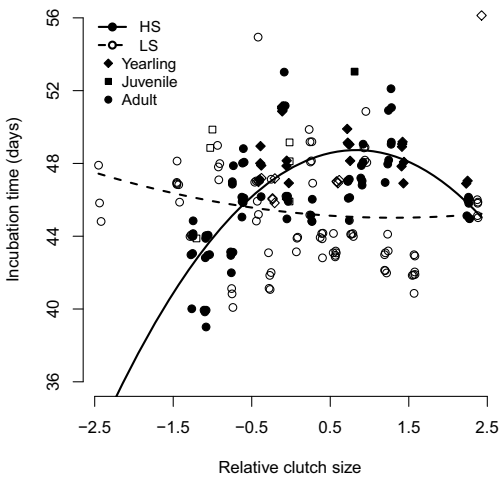


Figure 3.5 Incubation time by relative clutch size (Rclsize, i.e., female investment) depending on stochasticity treatment (HS, LS). Lines are predicted from the LMM. Symbols depict mother age class: circle: adults; diamond: released yearlings (current adults); square: released juveniles (current yearlings).

Discussion

The experimental manipulation of abiotic conditions predicted by future scenarios of climate change can provide valuable knowledge on the mechanisms that drive individual and population responses to environmental changes and thus improve our predictive capacity. In theoretical models, introducing environmental stochasticity reduces long-term population growth rates, and increases the probability of population extinction (Coulson and Godfray 2007). In accord with this idea, our results showed that increased stochasticity led to reduced survival probability in all three age classes of the population (Table 3.1).

In stochastic environments, productivity is expected to vary with time, potentially alternating between periods of

over-abundance and scarcity. The periodicity of these productivity pulses strongly depends on environmental abiotic conditions (Sears et al. 2004). Precipitation stochasticity produces fluctuations in habitat humidity, which in turn affect prey availability, prey diversity and habitat quality (Kardol et al. 2011; Lorenzon et al. 2001; Tsiafouli et al. 2005). For short-lived organisms, short-term temporal deprivation of resources can have a significant impact (e.g., Le Galliard et al. 2005a; Massot and Aragon 2013). Furthermore, food shortage leads to a reduction of energy stores (Schultner et al. 2013), suggesting that in stochastic environments, stored lipids may importantly decline during periods of scarcity (Avery 1970).

The reduction of resource abundance also increases the level of intra-population competition (Benton and Beckerman 2005), which may constrain the acquisition of energy. Younger *Z. vivipara* have a lower amount of fat reserves per unit body weight and a higher metabolic rate than adults (Avery 1974), and asymmetric inter-cohort competition exists between juveniles and older individuals due to differential body sizes (Massot et al. 1992; Mugabo et al. 2010). Thus, intensified contest competition for food/water resources and space in HS populations and the depletion of fat stores may have been responsible for increased mortality of juveniles and yearlings (Mugabo et al. 2011). Juvenile and yearling survival have a direct impact on recruitment and increased mortality may negatively affect the future breeding population size, thus population growth (De Roos et al. 2003; Steiner et al. 2014). The fact that adult survival was also affected by stochasticity suggests that intra-cohort competition was also present, at least within this cohort. Adult survival varies little within the year (Heulin et al. 1997), but has a large effect on population growth rate (Boyce et al. 2006; Pfister 1998). Increased adult mortality may lead to population decline and increase the chance of population extinction in the long-term, in agreement with the theoretical predictions of increased stochasticity (Drake 2005; Saether and Engen 2004).

The effects of stochasticity on survival probability were also sex specific in juveniles. Thus not only population size, but also population structure, may be affected by increased stochasticity. Male juveniles survived better than females in LS populations and females survived similarly in LS and HS (Figure 3.3). If male and female juveniles of *Z. vivipara* have similar energetic requirements, as has been suggested (Le Galliard et al. 2005a), this effect cannot be explained by intra-cohort competition for food. In

contrast, it may result from sex-specific inter-cohort agonistic social interactions. In other words, males and females may experience different levels of competition within the same social environment (Lecomte et al. 1994). As a consequence of sex-specific survival, climatic stochasticity may eventually lead to altered sex-ratios in the population. Irrespective of population size, adult sex-ratio can further affect survival probability in a sex-specific manner, intensifying the sex bias and increasing the risk of population collapse (Le Galliard et al. 2005b). For example, it has been shown that in male-biased populations, female common lizards suffer from reduced survival and reproductive success (Fitze et al. 2005; Le Galliard et al. 2005c).

Contrary to what is commonly found in wild populations, adult males survived better than females (Heulin et al. 1997; Pilorge 1981). Because our experimental system prevented the presence of predators, this result suggests that predation may be an important cause of male mortality in natural populations (Clobert et al. 2000). In support of this idea, adult males have longer activity periods (Bauwens 1981), higher catchability (Bauwens and Thoen 1981), and they are more mobile than females during reproductive season, all of which increase the risk of predation (Magnhagen 1991). Moreover, male-biased predation is common among some typical *Z. vivipara* predators (Christe et al. 2006).

In yearlings, ISVL was negatively correlated with survival in females, but not in males. Given that yearling final SVL was correlated with ISVL, and sexual maturity is size-dependent, initially larger female yearlings might have been the target of male harassment in spring; however, their smaller sizes relative to adult females may have impaired their capacity to cope with male aggression during copulation attempts, imposing high fitness costs (Fitze and Le Galliard 2008; Heulin 1988; Le Galliard et al. 2005c). Alternatively, larger individuals may require more food and water for maintenance than smaller ones (Hulbert and Else 2004), which would make them more vulnerable to the scarcity of resources. Since *Z. vivipara* is a sexually dimorphic species, male and smaller female yearlings would have similar sizes, which would explain why this correlation was only found in females.

Because juveniles and yearlings allocate most of their energy to growth, growth rate should be particularly susceptible to environmental changes in both age classes (Pilorge et al. 1987). Accordingly, juvenile and yearling growth rates were significantly different among treatments at least for one time period.

The occurrence of extreme events was only relevant to yearlings, although its effects usually depended on the level of stochasticity (Figure 3.1) or the individual's sex. Nevertheless, final SVL was not affected by treatments, suggesting life-history plasticity and the existence of compensatory patterns of growth in both cohorts (Lorenzon et al. 2001; Mugabo et al. 2011; Mugabo et al. 2010; Sorci et al. 1996a). In LS populations, adults grew faster between release and August, an important period of resource acquisition and build-up of fat reserves (Avery 1974), suggesting that reduced environmental stochasticity allows for a more consistent feeding. Only females were affected by stochasticity from August to September, and from September to June, males grew slower than females in every treatment combination except in the most stable (predictable) of all (LS, nE; Figure 3.2). These differences between sexes may be explained by differential patterns of acquisition or allocation of resources to functions (e.g., towards reproduction and intra-sexual competition instead of growth in males).

We found no differences among treatments in the proportion of reproducing females. Only age class determined the probability of being gravid, with released adults and yearlings more likely to reproduce than juveniles, as expected. However, in absolute terms, the number of produced clutches was higher in LS populations. Since only the first reproductive attempt was taken into account (i.e., the first clutch), the higher clutch production was not the result of differences in fecundity but of higher survival probabilities of potentially reproductive females in LS populations. Additionally, clutch size was not affected by treatments. In *Z. vivipara*, most of the intra-population variance in clutch size is attributable to female size and genetic causes (Bauwens and Verheyen 1987; Shine 2005). Thus, population declines could not be easily compensated through changes in e.g., the number of offspring (Stearns 1992). Overall, the fact that adults and yearlings were as likely to produce a clutch, that clutch size was not significantly affected by treatments, only by body size, and that final SVL was significantly larger in adults from LS populations, suggest that reproductive output in HS populations may be lower than in LS populations, which confers the former a higher risk of population decline.

With respect to the timing of reproduction, we found earlier laying dates in adults and yearlings compared to juveniles. These age differences could be attributed to individual physiological conditions related to size and are in line with sexual maturation being size-dependent (Bauwens 1999; Bauwens and

Verheyen 1985; Heulin 1985b). Juveniles may need additional growth before reaching the minimum size necessary for reproduction, thus delaying the time of clutch production. Additionally, we found earlier laying dates in HS populations, supporting that the timing of reproduction is influenced by environmental factors, which may confer great adaptive potential (Bauwens and Verheyen 1985; Heulin et al. 1994; Olsson and Shine 1997; Roig et al. 2000).

Early hatching is advantageous because it provides more time for juveniles to grow and store energy before hibernation, which is associated with increased juvenile wintering survival (Bauwens 1981; Bauwens and Verheyen 1985; Bauwens and Verheyen 1987). Consistent with this, we found that hatching date was negatively correlated with juvenile survival, irrespective of treatments. Other than laying date, hatching date may depend on the length of the incubation period. Incubation time varied with female reproductive effort (Rclsize) only in HS populations and Rclsize showed a non-linear relationship with incubation time (Figure 3.5). Interestingly, Rclsize was also significantly higher in HS populations. Because we incubated all the eggs under a constant environment and in the absence of predators, these differences in incubation time cannot be explained by incubation conditions. Altogether, the results on laying date, incubation time and Rclsize point to a strategy adopted by females in HS populations in response to more unpredictable environmental conditions to lay earlier in the season and have shorter incubation times, at the expense of increased reproductive effort, presumably to guarantee better juvenile survival (see above) and/or the opportunity to lay several clutches in a single activity season (e.g., a bet-hedging strategy; Adolph and Porter 1996). This could, however, negatively affect future reproductive attempts because current and future reproductive effort trade-off in this species (Bleu et al. 2013).

Yearlings, possibly reproducing for the first time, showed higher reproductive effort than adults and higher reproductive effort is positively correlated to hatchling/reproductive success (Romero-Diaz unpubl. data; Sinervo 1990). This result supports the existence of alternative reproductive strategies in different age classes (Richard et al. 2005), and is in line with the hypothesis that selection on reproductive performance is stronger earlier in life than later in life (Stearns 1992).

Here we have shown that climatic stochasticity influences population dynamics of *Z. vivipara* through effects on life-history traits of individuals from all

cohorts. The biological mechanisms involve the interplay of density-independent (climatic stochasticity) and density-dependent processes (competition) that result in intra-population variation in growth, survival and reproductive success. Our results were in agreement with the main theoretical predictions of increased environmental stochasticity, namely long-term population decline and increased risk of extinction. This and previous studies on common lizards have revealed the species' potential for adaptation through plasticity of life-history traits (Adolph and Porter 1993; Lorenzon et al. 2001; Lorenzon et al. 1999). However, our results suggest that there are limits to the capacity of individuals to cope with increased climatic stochasticity.

We hypothesize that it is unlikely that the here shown direct, negative effects on individual fitness (e.g., survival) could be rapidly counteracted at the population level through, e.g., increased fecundity or relaxed intra-population competition after a population decline, for several reasons. First, the negative effects of poor years on population growth are greater than the positive effects of good years and stochastic effects are often temporally correlated (Coulson and Godfray 2007). Second, there may be other delayed negative effects of stochasticity on individual performance on subsequent seasons or even on the following generations (Mugabo et al. 2010; chapter I). Third, depending on the population size, additional effects such as demographic stochasticity, Allee effects, or inbreeding depression may further contribute to population declines. Finally, because population structure is also disturbed (e.g., sex-ratios), there would be a higher risk of population instability, regardless of population size. In conclusion, we demonstrate that increased stochasticity of habitat humidity is a climate-change related factor that could potentially act as a proximate mechanism in the distributional shift projected for *Z. vivipara* in the upcoming decades, although presumably not the only one. Future studies should consider simultaneously the effects of different environmental factors because, as it has been suggested, the environmental changes produced by different aspects of climate change may have opposite effects in the dynamics of populations (Drake 2005).

Acknowledgements. We are very thankful to M. Peñalver Alcázar for technical support. M.C. Breedveld kindly provided some graphic material. C.R.D was supported by the Spanish Ministry of Education (FPU program) grant number AP2009-0350. Funding was provided by the Spanish Ministry of Education and Science (grant numbers CGL2008-01522, CGL2012-32459) and the Swiss National Science Foundation (grant numbers

PPOOP3_128375, PP00P3_152929/1) to P.S.F. Capture and experimentation licenses were approved by the Gobierno de Aragón and Navarra (refs: EHV/ 24/2010/105 & 106; LCE/mp 24/2012/426, and order numbers 577 & 670). The conducted study complies with current Spanish laws and with ASAB/ABS Guidelines for the Treatment of Animals in Behavioral Research.

REFERENCES

Adolph, S. C., and W. P. Porter. 1993. Temperature, activity, and lizard life-histories. American Naturalist 142:273-295.

—. 1996. Growth, seasonality, and lizard life histories: Age and size at maturity. Oikos 77:267-278.

Anderson, R. M., and R. M. May. 1978. Regulation and stability of host-parasite population interactions: I. Regulatory processes. Journal of Animal Ecology 47:219-247.

Araújo, M. B., F. Guilhaumon, D. R. Neto, I. Pozo, and R. Calmaestra. 2011, Impactos, Vulnerabilidad y Adaptación al Cambio Climático de la Biodiversidad Española. 2 Fauna de Vertebrados: Proyecciones de las áreas de distribución potencial de la fauna de vertebrados de la España peninsular por efecto del cambio climático. Madrid, Dirección general de medio Natural y Política Forestal. Ministerio de Medio Ambiente, y Medio Rural y Marino.

Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712–1728.

Avery, R. A. 1970. Utilization of caudal fat by hibernating common lizards, *Lacerta vivipara*. Comparative Biochemistry and Physiology 37:119-121.

—. 1975a. Age-structure and longevity of Common lizard (*Lacerta vivipara*) populations. Journal of Zoology 176:555-558.

—. 1975b. Clutch size and reproductive effort in the lizard *Lacerta vivipara* Jacquin. Oecologia 19:165-170.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-4. http://CRAN.R-project.org/package=lme4.

Bauwens, D. 1981. Survivorship during hibernation in the european common lizard, *Lacerta vivipara*. Copeia 1981:741-744.

—. 1999. Life-history variation in lacertid lizards. Natura Croatica 8:239-252.

Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard Lacerta vivipara. Journal of Animal Ecology 50:733-743.

Bauwens, D., and R. F. Verheyen. 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. Journal of Herpetology 19:353-364.

—. 1987. Variation of reproductive traits in a population of the lizard *Lacerta vivipara*. Holarctic Ecology 10:120-127.

Benton, T. G., and A. P. Beckerman. 2005. Population dynamics in a noisy world: Lessons from a mite experimental system, Pages 143-181

Advances in Ecological Research, Academic Press.

Benton, T. G., S. J. Plaistow, and T. N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B: Biological Sciences 273:1173-1181.

Bleu, J., J.-F. Le Galliard, P. S. Fitze, S. Meylan, J. Clobert, and M. Massot. 2013. Reproductive allocation strategies: a long-term study on proximate factors and temporal adjustments in a viviparous lizard. Oecologia 171:141-151.

Boyce, M. S., C. V. Haridas, C. T. Lee, and the NCEAS Stochastic Demography Working Group. 2006. Demography in an increasingly variable world. Trends in Ecology & Evolution 21:141-148.

Braña, F. 1996. Sexual dimorphism in lacertid lizards: Male head increase vs female abdomen increase? Oikos 75:511-523.

Breedveld, M. C., and P. S. Fitze. 2015. A matter of time: delayed mate encounter postpones mating window initiation and reduces the strength of female choosiness. Behavioral Ecology and Sociobiology 69:533-541.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Yeong Ryu, G. C. Sbeglia et al. 2013. How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences 280.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.

Clobert, J., A. Oppliger, G. Sorci, B. Ernande, J. G. Swallow, and T. G. Jr. 2000. Trade-offs in phenotypic traits: Endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. Functional Ecology 14:675–684.

Coulson, T., T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall, and J. M. Gaillard. 2006. Estimating individual contributions to population growth: evolutionary fitness in ecological time. Proceedings of the Royal Society B-Biological Sciences 273:547-555.

Coulson, T., and H. C. J. Godfray. 2007. Single-species dynamics, Pages 257 *in* R. M. May, and A. R. McLean, eds. Theoretical Ecology: Principles and Applications. UK, Oxford University Press.

Christe, P., L. Keller, and A. Roulin. 2006. The predation cost of being a male: implications for sex-specific rates of ageing. Oikos 114:381-384.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond Predictions: Biodiversity conservation in a changing climate. Science 332:53-58.

De Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473-487.

Drake, J. M. 2005. Population effects of increased climate variation. Proceedings of the Royal Society B: Biological Sciences 272:1823–1827.

Dublin, L. I., and A. J. Lotka. 1925. On the true rate of natural increase: As exemplified by the population of the

United States, 1920. Journal of the American Statistical Association 20:305-339.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: Observations, modeling, and impacts. Science 289:2068-2074.

Ehrlich, P. R., D. D. Murphy, M. C. Singer, C. B. Sherwood, R. R. White, and I. L. Brown. 1980. Extinction, reduction, stability and increase: The responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. Oecologia 46:101-105.

Fitze, P. S., and J.-F. Le Galliard. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. Ecology Letters 11:432-439.

Fitze, P. S., J.-F. Le Galliard, P. Federici, M. Richard, and J. Clobert. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. Evolution 59:2451-2459.

Grenot, C., B. Heulin, T. Pilorge, M. Khodadoost, A. Ortega, and Y. P. Mou. 1987. Water budget in some populations of the European common lizard, *Lacerta vivipara* Jacquin. Functional Ecology 1:131-138.

Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and B. T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71-75.

Heulin, B. 1985b. Maturité sexuelle et âge à la première reproduction dans une population de plaine de *Lacerta vivipara*. Canadian Journal of Zoology 63:1773-1777.

—. 1988. Observations sur l'organisation de la reproduction et sur les comportements sexuels et agonistiques chez *Lacerta vivipara*. Vie Milieu 38.

Heulin, B., K. Osenegg-Leconte, and D. Michel. 1997. Demography of a bimodal reproductive species of lizard (*Lacerta vivipara*): Survival and density characteristics of oviparous populations. Herpetologica 53:432-444.

Heulin, B., K. Osenegg, and D. Michel. 1994. Survie et incubation des oeufs dans deux populations ovipares de *Lacerta vivipara*. Amphibia-Reptilia 15:199-219.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65-70.

Hulbert, A. J., and P. L. Else. 2004. Basal metabolic rate: history, composition, regulation, and usefulness. Physiological and Biochemical Zoology 77:869-876.

IPCC. 2013. Summary for policymakers *in* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels et al., eds. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, NY, USA., Cambridge University Press.

—. 2014a. Annex II: Glossary, Pages 1757-1776 *in* V. R. Barros, C. B. Field, D. J.

Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee et al., eds. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jiguet, F., A.-S. Gadot, R. Julliard, S. E. Newson, and D. Couvet. 2007. Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biology 13:1672-1684.

Johst, K., and C. Wissel. 1997. Extinction risk in a temporally correlated fluctuating environment. Theoretical Population Biology 52:91-100.

Kardol, P., W. N. Reynolds, R. J. Norby, and A. T. Classen. 2011. Climate change effects on soil microarthropod abundance and community structure. Applied Soil Ecology 47:37-44.

Kerr, J. T., and H. M. Kharouba. 2007. Climate change and conservation biology, Pages 257 *in* R. M. May, and A. R. McLean, eds. Theoretical Ecology: Principles and Applications. UK, Oxford University Press.

Koons, D. N., C. J. Metcalf, and S. Tuljapurkar. 2008. Evolution of delayed reproduction in uncertain environments: a life-history perspective. American Naturalist 172:797-805.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911-927.

Le Galliard, J.-F., J. Cote, and P. S. Fitze. 2008. Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. Ecology 89:56-64.

Le Galliard, J.-F., R. Ferriere, and J. Clobert. 2005a. Juvenile growth and survival under dietary restriction: are males and females equal? Oikos 111:368-376.

Le Galliard, J.-F., P. S. Fitze, R. Ferrière, and J. Clobert. 2005c. Sex ratio bias, male aggression, and population collapse in lizards. Proceedings of the National Academy of Sciences of the United States of America 102:18231–18236.

Le Galliard, J.-F., O. Marquis, and M. Massot. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. Journal of Animal Ecology 79:1296-1307.

Lecomte, J., J. Clobert, M. Massot, and R. Barbault. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. Ecoscience 1:300-310.

Lorenzon, P., J. Clobert, and M. Massot. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. Evolution 55:392-404.

Lorenzon, P., J. Clobert, A. Oppliger, and H. John-Alder. 1999. Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). Oecologia 118:423-430.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. Trends in Ecology & Evolution 6:183-186.

Marion, G., E. Renshaw, and G. Gibson. 2000. Stochastic modelling of environmental variation for biological populations. Theoretical Population Biology 57:197-217.

Massot, M., and P. Aragon. 2013. Phenotypic resonance from a single meal in an insectivorous lizard. Current Biology 23:1320-1323.

Massot, M., J. Clobert, T. Pilorge, J. Lecomte, and R. Barbault. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. Ecology 73:1742-1756.

Milá, B., Y. Surget-Groba, B. Heulin, A. Gosa, and P. S. Fitze. 2013. Multilocus phylogeography of the common lizard *Zootoca vivipara* at the Ibero-Pyrenean suture zone reveals lowland barriers and high-elevation introgression. BMC Evolutionary Biology 13:192.

Mugabo, M., O. Marquis, S. Perret, and J.-F. Le Galliard. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. Journal of Evolutionary Biology 23:1886 - 1898.

—. 2011. Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. Oecologia.

Olsson, M., and R. Shine. 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): Why early clutches are better. Journal of Evolutionary Biology 10:369-381.

Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R. Scheffers et al. 2015. Assessing species vulnerability to climate change. Nature Climate Change 5:215-224.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change, Pages 637-669 Annual Review of Ecology Evolution and Systematics.

Parmesan, C., T. L. Root, and M. R. Willig. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81:443-450.

Peñalver-Alcázar, M., C. Romero-Diaz, and P. S. Fitze. 2015. Communal egg-laying in oviparous *Zootoca vivipara louislantzi* of the Central Pyrenees. Herpetology Notes 8:4-7.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences of the United States of America 95:213-218.

Pilorge, T. 1981. Structure et dynarnique d'une population du lézard vivipare. Signification adaptive de la viviparité chez les lézards. Bulletin de la Societé Herpetologique de France 18:29-31.

Pilorge, T., and J. Castanet. 1981. Age determination in a wild population of the European viviparous lizard (*Lacerta vivipara*, Jacquin, 1787). Acta Oecologica-Oecologia Generalis 2:3-16.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and t. R. D. C. Team. 2013. nlme: Linear and Nonlinear Mixed

Effects Models. R package version 3.1-108.

Richard, M., J. Lecomte, M. de Fraipont, and J. Clobert. 2005. Age-specific mating strategies and reproductive senescence. Molecular Ecology 14:3147-3155.

Roig, J. M., M. A. Carretero, and G. A. Llorente. 2000. Reproductive cycle in a Pyrenean oviparous population of the common lizard (*Zootoca vivipara*). Netherlands Journal of Zoology 50:15-27.

Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology & Evolution 12:143-149.

Saether, B. E., and S. Engen. 2004. Stochastic population theory faces reality in the laboratory. Trends in Ecology & Evolution 19:351-353.

Saltz, D., D. I. Rubenstein, and G. C. White. 2006. The impact of increased environmental stochasticity due to climate change on the dynamics of asiatic wild ass. Conservation Biology 20:1402-1409.

Samhouri, J. F., M. A. Steele, and G. E. Forrester. 2009. Inter-cohort competition drives density dependence and selective mortality in a marine fish. Ecology 90:1009-1020.

Schultner, J., A. S. Kitaysky, J. Welcker, and S. Hatch. 2013. Fat or lean: adjustment of endogenous energy stores to predictable and unpredictable changes in allostatic load. Functional Ecology 27:45-55.

Sears, A. L. W., R. D. Holt, and G. A. Polis. 2004. Feast and famine in food webs: the effects of pulsed productivity *in* G. A. Polis, M. E. Power, and G. R. Huxel, eds. Food Webs at the Landscape Level, University of Chicago Press.

Shine, R. 2005. Life-history evolution in reptiles, Pages 23-46 Annual Review of Ecology Evolution and Systematics. Annual Review of Ecology Evolution and Systematics. Palo Alto, Annual Reviews.

Sinervo, B. 1990. The evolution of maternal investment in lizards: An experimental and comparative analysis of egg size and its effects on offspring performance. Evolution 44:279-294.

Sorci, G., J. Clobert, and S. Belichon. 1996a. Phenotypic plasticity of growth and survival in the common lizard *Lacerta vivipara*. Journal of Animal Ecology 65:781-790.

Stearns, S. C. 1992, The evolution of life histories. Oxford, UK, Oxford University Press.

Steiner, U. K., S. Tuljapurkar, and T. Coulson. 2014. Generation time, net reproductive rate, and growth in stage-age-structured populations. American Naturalist 183:771-783.

Thomas, C. D., M. C. Singer, and D. A. Boughton. 1996. Catastrophic extinction of population sources in a butterfly metapopulation. American Naturalist 148:957-975.

Tsiafouli, M. A., A. S. Kallimanis, E. Katana, G. P. Stamou, and S. P. Sgardelis. 2005. Responses of soil microarthropods to experimental short-term manipulations of soil moisture. Applied Soil Ecology 29:17-26.

West-Eberhard, M. J. 2003, Developmental Plasticity and

Evolution, Oxford University Press, USA.
Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009, Mixed effects models and extensions in ecology with R. New York, NY, USA, Springer.

SUPPLEMENTARY MATERIAL

Table S3.1: Observations of daily precipitation during the summer months recorded by the Spanish State Meteorological Agency (AEMET) from 1951 to 2010 at the "Huesca/Pirineos" meteorological station (42° 05' 00.1" N, 0° 19' 35.0" W). The magnitude of intense precipitation events (>15mm/h < 30mm/h) established by AEMET is based on historical observations over national territory.

	June	July	August	September	Total
Days with data	1715	1805	1757	1752	7029
Days with precipitation (> 0 mm)	431	270	291	374	1366
Days with potential intense (or above intense) precipitation events (> 15 mm/day)	57	20	43	58	178
Maximum frequency of intense (or above) precipitation events	3.3%	1.1%	2.5%	3.3%	2.5%
Maximum frequency of intense (or above) precipitation events with respect to days with precipitation	13.2%	7.4%	14.8%	15.5%	13%
Maximum per year average of days with intense (or above) precipitation	0.97	0.34	0.73	0.98	3.01

Chapter III

Social and abiotic cues affect context-dependent mate choice and contribute to the maintenance of a color polymorphism

Cristina Romero-Diaz, Hanna Kokko,
& Patrick S. Fitze

ABSTRACT

Genetic variation (polymorphisms) can be maintained by frequency-dependent (FD) sexual selection. Recent evidence suggested that rock-paper-scissors (RPS) frequency cycles observed in polymorphic common lizard males (*Z. vivipara*) are generated by FD (context-dependent) female mate choice, reinforced by FD selection on offspring survival, yet few experimental evidence exists. To test how FD selection is determined we set up *Z. vivipara* populations differing in male morph frequency and the abiotic environment. We then modeled different mating patterns allowing for different types of sexual selection and tested their fit with the experimental data. The relative competitiveness (i.e., reproductive success) of male morphs was best explained by FD inter-sexual selection, which was mainly driven by the morph frequency of the maturing cohort, and by interactive effects of the abiotic environment. These results highlight the importance of social and abiotic factors for the maintenance of polymorphisms, might explain why frequency cycles are generally irregular and spatially synchronous, and why polymorphic geographic variation across a species' range exists. They also suggest that environmental change (e.g., climate) may affect the maintenance and evolution of polymorphisms.

Keywords: Frequency-dependent sexual selection, reproductive strategies, color polymorphism, morph reproductive success, lizard.

Sexual selection is an important process driving rapid, divergent evolution of secondary sexual traits (Andersson 1994; Darwin 1871; Kirkpatrick 1982; Lande 1981). Sexual selection can be strongly directional, e.g., through "runaway selection" (Fisher 1930), depleting genetic variation. However, condition-dependent mechanisms, genotype by environment interactions, as well as mechanisms of balancing selection may slow divergent evolution and lead to the maintenance of genetic variation (e.g., Grafen 1990; Sinervo and Lively 1996; Tolle and Wagner 2011). Alternative mating or reproductive strategies (i.e., polymorphisms) exist in a diversity of animal and plant species (Fleming 1996; Gross 1996; Mayer and Charlesworth 1991; Roulin 2004; Shuster and Wade 1991; Sinervo and Lively 1996; Werren and Charnov 1978) illustrating the maintenance of genetic variation.

Theory poses that polymorphisms can persist over time due to frequency-dependent (FD) sexual selection (Kokko et al. 2007; Sinervo and Calsbeek 2006), a way of non-random mating in which the fitness of one morph depends on its frequency relative to that of alternative morphs in the population (Ayala and Campbell 1974; Fisher 1930). Negative

FD selection (FDS) can maintain polymorphisms by means of a mating advantage of rare types, and negative FDS is often coupled to positive FDS, generating highly complex dynamics. The latter arise either due to rare morph advantage combined with self-type mate preference (i.e., assortative mating; e.g., Kokko et al. 2014) or cooperation/altruism to self-types (e.g., Rock-Paper-Scissors dynamics; Sinervo and Calsbeek 2006; Sinervo et al. 2006; Sinervo et al. 2007). Key mechanisms potentially explaining negative FDS include, among others, context-dependent sexual selection, negative FD survival selection, and genotype by environment interactions, all of which may crucially depend on environmental conditions (e.g., climate, food and mate availability, intensity of competition). For example, abiotic conditions may affect the morphs' fitness payoffs and thereby lead to the predominance of different morphs in different environmental conditions (Roulin 2004). Moreover, the effects of environmental conditions may be additive or interactive, the latter potentially explaining the commonly observed deviations from theoretic model predictions, such as the irregular orbits exhibited by frequency cycles (e.g., Sinervo and Lively 1996). Despite the numerous observations being congruent with FDS in nature (Kokko and Rankin 2006; Shuster and Wade 2003) and the suggested impact of environmental conditions, experimental evidence for negative FD mechanisms maintaining polymorphisms and the effects of the environment on FDS remain scarce (Sinervo and Calsbeek 2006).

Here we experimentally tested the relevance of environmental conditions for models explaining the temporal maintenance of genetic variation, using the European common lizard (*Zootoca vivipara*) as a model species. Male *Z. vivipara* exhibit a ventral color polymorphism that is associated with alternative mating strategies, similarly to other color-polymorphic species (reviewed in Neff and Svensson 2013). *Z. vivipara* males exhibit six color phenotypes consistent with a single locus with three alleles (orange, *o*, yellow, *y*, and white, *w*), yielding six putative color genotypes: *ww*, *wy*, *wo*, *yy*, *yo*, and *oo* (Sinervo et al. 2007). Color alleles are linked with endurance and body size: body size of *o* and *w* males is larger than that of *y* males, and *o* alleles confer higher, size-independent endurance compared to *w* and *y*, whereas *w* confers high endurance through allometry compared to *y* (Sinervo et al. 2007). The morphs' performance differences and the color morph frequency-dependent recruitment of the offspring generate Rock-Paper-Scissors (RPS) dynamics where the *o* strategy beats

o strategy beats *w*, *w* beats *y* and *y* beats *o* (San-Jose et al. 2014; Sinervo et al. 2007), which are congruent with the rapid morph frequency cycles observed in wild populations (Sinervo et al. 2007). These observed frequency cycles advance in the correct direction but their orbits are generally irregular (Fig. 5b in Sinervo et al. 2007), despite the rather regular model predictions (and Fig. 7 in Sinervo et al. 2007; Fig. 4b in Sinervo and Lively 1996); nevertheless, some synchronization may exist among close populations, keeping them in phase (Fig. 5c in Sinervo et al. 2007).

A recent experiment demonstrated that morph frequency cycles are generated by two independent, cumulative FD selective episodes: negative FD sexual selection reinforced by FD offspring survival (San-Jose et al. 2014; Sinervo et al. 2007). The observed FD sexual selection may be the result of two mechanisms. First, as suggested in *Uta stansburiana* (Sinervo and Lively 1996), intra-sexual competition among adult male color morphs may impose negative FD sexual selection. Second, FD sexual selection can also be produced by inter-sexual selection (e.g., Fitze et al. 2014; Sinervo et al. 2007), and more specifically, by context-dependent female mate choice (Fitze et al. 2014; San-Jose et al. 2014; Sinervo et al. 2007). Context-dependent female mate choice is frequently based on cues from the social and abiotic environment (Alonzo and Sinervo 2001; Shuster and Wade 2003) and on male traits, including male color morph, body size and body condition (Fitze et al. 2008). Given that color morph is associated with body size and performance (see above) and thus with traits signaling male quality, these traits, rather than male color morph, may explain male reproductive success and the observed patterns of negative FD sexual selection. Moreover, abiotic environmental conditions may affect the morphs' fitness payoffs and performance (Roulin 2004). In other words, there may be different effects of a given environmental condition on each morph (i.e., an interactive effect). For example, bigger morphs that need more resources for maintenance may have an advantage in food-rich environments, and a disadvantage in food-poor environments, while the opposite might be true in smaller morphs.

To disentangle between mechanisms of selection and to determine the role of environmental conditions, we manipulated adult male color morph frequency and environmental conditions in semi-natural populations using a 3 x 2 factorial design. We tested whether and how environmental conditions affect sexual selection and investigated the prevailing mating pattern (i.e., random

mating, simple non-random mating, FD mating, environment-dependent FD mating) and the traits involved in sexual selection. More specifically, we tested whether the observed sexual selection is affected by male color morph or rather by associated traits (i.e., SVL and body condition; Sorci et al. 1996a). We also tested whether the selection depends on abiotic conditions, either additively or interactively. To test among types of sexual selection we manipulated population color morph frequency of adult males, but not of the maturing male cohort (i.e., the yearlings). If intra-sexual selection is responsible for the imposed selection, we predicted that adult male color morph frequency will predict male competitiveness best and that the maturing male's color morph frequency will be of minor or no importance, given that maturing males are not competing for access to females. In contrast, if inter-sexual selection is important, we predicted that both, the maturing and the adult male's color morph frequency will be important, since maturing males become adults in summer, and take part in juvenile survival selection in autumn. This prediction stems from theoretic models and experimental results (Fitze et al. 2014; San-Jose et al. 2014; Sinervo et al. 2007), which indicate that females choose mate partners in order to optimize offspring survival (i.e., survival in autumn). To disentangle among hypotheses, we modeled the different mating patterns, traits and abiotic conditions, assessed their fit to the experimental data and tested their importance using an information theoretic approach.

MATERIALS AND METHODS

Study species

Z. vivipara is a small (adult snout-to-vent length, SVL: 45-70 mm) lacertid widely distributed across Eurasia. It inhabits hygrophilic and mesophilic habitats including moist heathlands and peat bogs. Environmental humidity importantly limits growth, condition, survival and reproduction of *Z. vivipara* (Le Galliard et al. 2010; Lorenzon et al. 2001; Lorenzon et al. 1999; Marquis et al. 2008), because of the species' high rate of evaporative water loss (Grenot and Heulin 1990; Grenot et al. 1987).

Individuals emerge from hibernation between March and May and they enter hibernation between late September and October (Roig et al. 2000). Sexual maturity is reached at about 2 years of age and reproduction begins immediately after female emergence from hibernation (Breedveld and Fitze 2015). Their reproductive system is polygynandrous (Fitze et al. 2005; Richard et al. 2005). The average lifespan of *Z. vivipara* is 2.8 years (Strijbosch and Creemers 1988) and

once survived the first year, it is 4 - 5 years (Avery 1975a; Pilorge and Castanet 1981; Sorci et al. 1996b). Maximum observed lifespan is 7 years for males and 11 years for females (Richard et al. 2005). Juvenile mortality is considerably high during the first year of life (Avery 1975a). Sub-adults (< 2 years) and adults survive with a similar probability (Heulin et al. 1997) and adult males generally survive worse than females (Heulin et al. 1997; Richard et al. 2005). There exists important generational overlap and populations are age-structured. In the Pyrenean populations males exhibit 6 alternative color morphs as described above, and females exhibit no color morphs (Arribas 2009).

Experimental system

Lizard populations were maintained in twelve semi-natural outdoor enclosures (100 m^2), which consisted of planted natural grassland, two water ponds, four stone piles and several logs that provided lizards with basking sites, shelters and hibernation burrows. Each population consisted of 20 adults (i.e., ≥ 2 years old; males n = 8, females n = 12), 5 to 6 yearlings (i.e., 1 year old; males n = 2, females n = 3 - 4) and 18 to 20 newborn juveniles (population total n = 43 - 46). Lizards were individually marked by toe-clipping, weighted to the nearest mg and measured to the nearest mm upon release.

In May 2010, three adult color morph frequencies and two types of humidity conditions were established, using a 3 x 2 factorial design. Adult color morph frequency was biased towards *o* (orange), *y* (yellow), or *w* (white) predominance, and each of the frequencies was established in four populations. The maturing male morphs (i.e., yearlings) were randomly distributed and did not differ among treatments and populations. Two populations of each color morph treatment were exposed to higher, and the other two to lower habitat humidity. Habitat humidity was manipulated by irrigating each population twice a day (i.e., at 9 a.m. and 5:30 p.m.). At each irrigation, enclosures belonging to the higher humidity treatment (H) were sprinkled for 12, and those of the lower humidity treatment (L) for 5 minutes. Each irrigation was split into two shifts (H: 6 and 6 minutes; L: 3 and 2 minutes of irrigation). The second shift started 2 and 9 minutes (H and L treatment, respectively) after the end of the first shift. This procedure guaranteed that in all enclosures 14 minutes passed between the start and end of the irrigation and thus lizards of all treatments were exposed to the same treatment length. At the start of the experiment no initial differences existed in SVL or body condition among populations and treatments, across all ages (all P < 0.91).

Age-structure, density, sex ratio and habitat structure did not differ either.

Paternity assignment

In May 2011, females were recaptured at regular intervals to determine the stage of female gravidity by ventral palpation. Females in an advanced stage of gravidity were brought into the laboratory and housed in individual *terraria* containing peat soil as substrate, a shelter, a water pond, and a basking surface (rock). Light (photoperiod: 12 L: 12 D) and heat were provided by a 40W bulb and UV light was provided for 2 hours/day. Water was available *ad libitum* and females were fed different prey items every other day (namely larvae of *Galleria mellonella*, *Acheta domestica*, and *Lumbricus terrestris*). Twice a day *terraria* were inspected for laid clutches and these were incubated at 21°C during the day (i.e., 9 a.m. to 9 p.m.) and 19°C during the night (Heulin et al. 1997). All newborn juveniles were measured and a genetic sample was collected. Thereafter offspring were released in new standardized populations that did not differ in color morph frequency, i.e., in a common garden. This assured that observed differences among color morph treatments are due to sexual selection and could not have arisen due to differences in survival selection. Offspring were recaptured one year later (in May 2012) to quantify male competitiveness (for the precise definition see 'Model development and analysis'), which was calculated based on recruiting offspring, since only these contribute to RPS dynamics (Sinervo et al. 2007).

DNA was extracted from the collected genetic sample using a BioSprint 96 DNA Blood Kit (Qiagen, Hilden, Germany). Five highly polymorphic microsatellite DNA loci (Lv-3–19, Lv-4–72, Lv-4-alpha, Lv-4–115, Lv-4-X; Boudjemadi et al. 1999), were amplified using previously established methods (for details see Laloi et al. 2004). Since the genetic profile of all mothers and putative fathers was known, the paternity was assigned manually and the program Cervus 3.0 (Marshall et al. 1998) was used to verify the correctness of the attribution. All surviving offspring were successfully attributed to a single father and the paternity was used to quantify male reproductive success, based on which the male's competitiveness was modeled (see below).

Model development and analysis

To estimate the relative competitiveness effect of each allele, we first described a general model that allows for non-random mating, such that a male's competitiveness (which we scale such that it is linearly related to predicted mating success) can depend on his alleles as well as the population composition (i.e., the

frequency of *o*, *y* and *w* alleles). Each allele's contribution to a male's competitiveness is denoted C_o, C_y, or C_w for orange, yellow and white, respectively. Assuming linearity for simplicity, we modeled this as a function of the populations' relative allele frequencies (p_o, p_y, and p_w) using parameters α_i, β_i, and γ_i, where i = o, y, or w, for C_o, C_y, and C_w, respectively; parameters with a subscript "b" denote intercepts:

$$C_o = \alpha_b + \alpha_o p_o + \alpha_y p_y + \alpha_w p_w \quad (1)$$
$$C_y = \beta_b + \beta_o p_o + \beta_y p_y + \beta_w p_w \quad (2)$$
$$C_w = \gamma_b + \gamma_o p_o + \gamma_y p_y + \gamma_w p_w \quad (3)$$

In the simplest case, only adult male alleles might be used to determine the values of p_i. However, the maturing cohort's alleles predict the frequency cycle advance (San-Jose et al. 2014; Sinervo et al. 2007), and key for testing the relative roles of intra-sexual or inter-sexual selection. We therefore introduced a parameter *x*, ranging between 0 and 1, to allow yearling alleles to be included if $x > 0$. Here *x* describes the relative weight of yearling allele frequencies (i.e., of the maturing cohort; Y_i,) compared to adult allele frequencies (A_i), with $x = 0.5$ giving equal weight to both:

$$p_i = \frac{xY_i + (1-x)A_i}{x(Y_o + Y_y + Y_w) + (1-x)(A_o + A_y + A_w)} \quad (4)$$

Here p_i corresponds to the allelic frequencies used in equations (1) to (3), and A_i and Y_i to the adult and yearling allele frequencies of the experimental populations. Using these equations, we computed a relative competitiveness score (c_k) for each male that took part in the mating competition (i.e., all recaptured males as well as males that fertilized eggs, but died before recapture). Other males were not considered, given that common lizards cannot store sperm during hibernation (Bleu et al. 2011a; pers. obs.). Relative competitiveness is given by:

$$c_k = \frac{e^{(C_i + C_j)}}{\sum_{k=1}^{n} e^{(C_o + C_y + C_w)}} \quad (5)$$

where *i* and *j* are the individual's first and second color alleles (o, y or w; note that $i = j$ in the case of homozygotes), and *k* denotes the k^{th} individual in a population of *n* individuals. Consequently, for each population, the sum of all individual c values was 1.

Based on this general model we developed a set of nested candidate models describing our different hypotheses (Table 4.1). We started with three initial models of mating pattern: 'R', random mating; 'nR', simple non-random mating; and 'F', frequency-dependent non-random mating. Model R estimated no parameters. Model nR

included only the intercept in the estimation of C_i (equations 1-3), allowing for a baseline difference in mating success among morphs that is independent of the color allele frequency. Model F estimated c_k as a function of the individual color morph frequency relative to that of the other morphs (equations 1-5).

Additional models were built as alterations of the above R, nR and F models, by including up to three parameters that can potentially affect male competitiveness (Table 4.1): humidity, male body size, and male body condition. The abbreviations of the models (Table 4.1) reflect the factors that are included. Habitat humidity, which had been experimentally manipulated, was coded as 'H' (Table 4.1), and used in equations with 1 denoting higher, and 0 lower humidity. Its effects were modeled by adding parameters α_h, β_h, and γ_h to equations 1-3. We either constrained α_h to equal β_h and γ_h (we term this the additive model for humidity) or allowed them to differ from each other (termed the interaction model for humidity, as its effect may now differ depending on population composition). Male snout-to-vent-length (SVL, 'V' in Table 4.1) was taken as body size and male body condition ('B') was estimated as the residuals of the regression between SVL and body mass. Male body size (Fitze and Le Galliard 2008) and male body condition affect male mating success (Fitze et al. 2010; Fitze et al. 2008; Heulin 1988) and their effect might be independent of morph frequency.

Finally, in the set of F models, competitive interactions within and between alleles were considered to be either asymmetrical ('A') or symmetrical ('S'). In the presence of asymmetrical competitive interactions, an alleles' competiveness was allowed to differ among contexts (i.e., allele frequencies). In a model, this can be done by estimating coefficients that are allowed to differ between alleles of different color (i.e., in equations 1-3 and in 'FA', Table 4.1: $\alpha_i \neq \beta_i \neq \gamma_i$, i = o, y, w). We also included a more restrictive symmetrical option because the observed RPS dynamic for *Z. vivipara* suggests competitive interactions such that *o* beats *w*, *w* beats *y*, and *y* beats *o* and the magnitude of their effect is similar. Symmetrical competitive interactions ('FS' models, Table 4.1) were modeled by constraining coefficients to have the same value for all 'self' effects (an allele experiencing the effect of the frequency of itself; i.e., α_o, β_y, and γ_w in equations 1, 2, and 3, respectively), and likewise for the effect of alleles assumed to be 'better-than-self' (an allele experiencing the effect of the frequency of the allele that is expected to beat it; i.e., α_y, β_w, and γ_o in equations 1, 2, and 3, respectively), and

likewise for alleles that are 'worse-than-self' (i.e., α_w, β_o, and γ_y in equations 1, 2, and 3, respectively). This was coded using a common parameter, l, for self, better-than-self, and worse-than-self allele frequency effects, such that α_o, β_y, and γ_w were replaced by l_1; α_y, β_w, and γ_o by l_2 (note: *o* beats *w* and thus *o* performs better with respect to *w* (γ_o) compared to itself (α_o); Table S4.1), and α_w, β_o, and γ_y by l_3 (note: *o* loses against *y* and thus *o* performs worse with respect to *y* (β_o) compared to itself (α_o); see also Table S4.2).

In a variant of the FD structure we assumed that the presence of inferior competitors has a negligible effect on the focal allele's competitiveness (i.e., α_w in (1), β_o in (2) and γ_y in (3) were set to 0). Here an allele's relative competitiveness only depends on the frequency of the self and better-than-self alleles in the population. This alternative, termed 'inferior competitors negligible' (models with an 'I', Table 4.1) was modeled in combination with the assumption of symmetrical or asymmetrical competitive interactions (e.g., models FSI and FAI, respectively; Table 4.1).

Since a published RPS model for *Z. vivipara* (Sinervo et al. 2007) predicts that the magnitude of the interactions will not be fully symmetrical (Table S4.1*a*), we also modeled the competitive interactions suggested by earlier published evidence (hereafter denominated as 'proposed' frequency-dependence; 'FP'). In this model, the effects of the worse-than-self allele's frequency (i.e., α_w, β_o, and γ_y), the self-allele frequency on *w* (i.e., γ_w), and the better-than-self allele frequency on *o* allele competitiveness (i.e., α_y) were all assumed negligible, i.e., set to 0. The effects of the better-than-self allele's frequency were equivalent in *w* and *y* allele competitiveness (i.e., β_w equals γ_o), both parameters being replaced by l_4. Finally, self-allele effects on *o* and *y* allele competitiveness were allowed to differ from each other (i.e., $\alpha_o \neq \beta_y$; Table 4.1).

Model development and model fit were performed in MATLAB®, using Maximum Likelihood Estimation (MLE). The use of MLE together with a model selection procedure (calculation of AIC scores, Burnham and Anderson 2002) allowed us to quantify the relative importance of different hypotheses and mechanisms affecting sexual selection. The best x was determined using MLE and then used to assess the model fit. In all models, a data point (a recruited offspring with known sire) contributes an additive value $\ln(c_k)$ to the log-likelihood of the model, according to the identity (k) of the sire. If the model predicted a small relative competitiveness for the actual sire, then $\ln(c_k) << 0$. If, on the other hand, the model produced a good match

Table 4.1 Description of used nested candidate models. For each model the number of estimated parameters (K) and parameter nomenclature are given. (α_i): parameters related to *o* allele competitiveness; (β_i): parameters related to *y* allele competitiveness; (γ_i): parameters related to *w* allele competitiveness; l_1: effects of self-allele frequency; l_2: effects of better-than-self allele frequency; l_3 effects of worse-than-self allele frequency; l_4 effect of the better-than-self performing allele frequency in FP models; (*b*): intercept; (*B*): body condition; (*v*): SVL; (*h*): humidity.

Model	K	parameters	model description
FPIH	9	α_b, β_b, γ_b, α_o, β_y, l_3, l_4, α_h, β_h, γ_h	proposed frequency-dependent model explaining RPS cycles in *Z. vivipara* ($\beta_w = \gamma_o = l_4$); inferior competitors negligible ($l_3 = 0$); humidity is relevant
FSIH	8	α_b, β_b, γ_b, l_1, l_2, l_3, α_h, β_h, γ_h	frequency-dependent mating; symmetric; inferior competitors negligible ($\alpha_w = \beta_o = \gamma_y = l_3 = 0$); humidity is relevant
FPI	6	α_b, β_b, γ_b, α_o, β_y, l_3, l_4	proposed frequency-dependent model explaining RPS cycles in *Z. vivipara* ($\beta_w = \gamma_o = l_4$); inferior competitors negligible ($l_3 = 0$)
FAI	9	α_b, α_o, α_y, β_b, β_y, β_w, γ_b, γ_o, γ_w,	frequency-dependent mating; asymmetric; inferior competitors negligible ($\alpha_w = \beta_o = \gamma_y = 0$)
FSH	9	α_b, β_b, γ_b, l_1, l_2, l_3 α_h, β_h, γ_h,	frequency-dependent mating; symmetric; humidity is relevant
FSIHV	11	α_b, β_b, γ_b, l_1, l_2, l_3, α_h, β_h, γ_h, α_v, β_v, γ_v	frequency-dependent mating; symmetric; inferior competitors negligible ($l_3 = 0$); humidity and male snout-to-vent length (SVL) are relevant
FSIHB	11	α_b, β_b, γ_b, l_1, l_2, l_3, α_h, β_h, γ_h, α_B, β_B, γ_B,	frequency-dependent mating; symmetric; inferior competitors negligible ($l_3 = 0$); humidity and male body condition are relevant
nRH	6	α_b, β_b, γ_b, α_h, β_h, γ_h	simple non-random mating; humidity is relevant
nRHB	9	α_b, β_b, γ_b, α_h, β_h, γ_h, α_B, β_B, γ_B	simple non-random mating; humidity and male body condition are relevant
FSI	5	α_b, β_b, γ_b, l_1, l_2, l_3	frequency-dependent mating; symmetric; inferior competitors negligible ($l_3 = 0$)
FS	6	α_b, β_b, γ_b, l_1, l_2, l_3	frequency-dependent mating; symmetric
nRHV	9	α_b, β_b, γ_b, α_h, β_h, γ_h, α_v, β_v, γ_v	non-random mating; humidity and male snout-to-vent length (SVL) are relevant
FA	12	α_i, β_i, γ_i	frequency-dependent mating; asymmetric, i = b, o, y, w
nR	3	α_b, β_b, γ_b	simple non-random mating
R	0	-	random mating

between the competitiveness distribution and the identity of the actual sire, then $\ln(c_k)$ is closer to zero, leading to a better AIC value as a whole.

Model comparison was done using Akaike Information Criteria corrected for finite sample sizes (AICc; Burnham and Anderson 2002; Burnham et al. 2011; Johnson and Omland 2004). The model with the lowest AICc is considered the 'best' model and models with $\Delta s > 2.0$ AICc were considered to have a significantly lower support (Burnham and Anderson 2002). For model comparison, models with non-additive effects and models with an excessive number of parameters were discarded given their consistently poorer performance (i.e., poorer than the models reported in Table 4.2).

RESULTS

The random mating (R) and simple non-random mating (nR) models were least supported (Table 4.2). The best model without FD mating (nRH, rank 8th Table 4.2) differed by more than 3 AICc from the best fitting model, indicating little support. The three best supported models, FPIH, FSIH and FPI, differed by less than 2 AICc (Table 4.2). The evidence ratios w_{FPIH} / w_{FPI} and w_{FSIH} / w_{FPI} showed that FPIH and FSIH were 2.5 and 2.2 times more likely than FPI, respectively. FPIH was only 1.14 more likely than FSIH and thus there was a certain degree of uncertainty regarding the best model. These two models had very similar structures: they included FD mating, negligible effects of worse-than-self alleles, and assumed symmetrical effects of better-than-self alleles. In FPIH and FPI, symmetry of better-than-self effects was assumed for *y* and *w* alleles but not for *o* alleles, while in FSIH symmetry was assumed for all three alleles. The yearling morph frequency was of high importance ($x \geq 0.697$; Table 4.2) in all but two models, providing strong support for the hypothesis that yearling allele frequencies importantly affect male competitiveness.

The two best fitting models included habitat humidity. In general, models including habitat humidity had lower AICcs than those without it (Table 4.2) and their summed evidence ratio was 0.773/0.225 = 3.43 (Table 4.2). Moreover, excluding habitat humidity from the models led to worse model fits, despite being more parsimonious (Δ = 1.84, 5.55, 5.61, and 12.32 for FPIH vs. FPI, FSIH vs. FSI, FSH vs. FS, and nRH vs. nR, respectively; Table 4.2). All models including interactive habitat humidity (parameters allowed to differ between morphs) were much better than those including identical habitat humidity effects for all morphs (all $\Delta \geq$

Table 4.2 Comparison of the candidate models (see Table 4.1) and their fit to the observed male relative competitiveness. The corrected Akaike's information criterion (AICc), the difference between the AICc of the top model and the model considered (Δ_i), Akaike weights (w_i), and the estimated best x value are given for each model.

rank	model(i)	AICc	Δ_i	w_i	estimated x
1	FPIH	174.89	0.00	0.271	*
2	FSIH	175.16	0.26	0.237	0.9899
3	FPI	176.73	1.84	0.108	0.6970
4	FAI	176.95	2.06	0.097	0.7980
5	FSH	177.48	2.59	0.074	1 (set to 0.9999)
6	FSIHV	177.84	2.95	0.062	1 (set to 0.9999)
7	FSIHB	178.22	3.33	0.051	0.0505
8	nRH	178.25	3.36	0.050	any (set to 1)
9	nRHB	179.55	4.66	0.026	any (set to 1)
10	FSI	180.71	5.82	0.015	0.8586
11	FS	183.09	8.20	0.004	0.8586
12	nRHV	184.86	9.97	0.002	any (set to 1)
13	FA	185.33	10.43	0.001	0.7980
14	nR	190.57	15.68	0.000	any (set to 1)
15	R	202.26	27.37	0.000	any (set to 1)

*Several x were optimal: 0.3030, 0.2323, 0.1111, 0.0404, 0.0202

8.2; tested models: 1st, 2nd and 5th, Table 4.2).

The inclusion of body condition (in models FSIHB and nRHB) did not improve the fit. Compared to FSIH and nRH models, models including body condition had lower support: $\Delta = 3.07$ and $\Delta = 1.3$, respectively. This indicates that the FD model without body condition explained the observed mating pattern better. Models with body size (snout-to-vent length, SVL) ranked in position 6 and 12, and the inclusion of SVL led in every case to worse fits, $\Delta \geq 2.7$ (compared to models FSIH and nRH, ranking 2nd and 8th, Table 4.2). Interactive effects of habitat humidity and SVL led to much less supported

models (all $\Delta \geq 7.02$; models not shown). Of the considered environmental conditions and individual traits, only habitat humidity had a strong effect on male reproductive success and its effect differed for each allele's competitiveness (i.e., interactive; Table 4.1).

DISCUSSION

Negative FDS can explain the maintenance of genetic variation (Sinervo and Calsbeek 2006) and potential mechanisms producing negative FDS might be affected by environmental conditions. Nevertheless, the relative importance of environmental conditions on the mechanisms maintaining genetic variation has rarely been investigated. Here we experimentally tested whether and how environmental conditions affect the operation of negative FDS and simultaneously disentangled among different mechanisms of selection. To this end, we manipulated the adult color morph frequency of populations and exposed them to different humidity regimes using a 3 x 2 factorial design. We modeled different mating patterns and hypotheses, and tested their relevance based on the relative competitiveness (i.e., reproductive success) of adult males, assessed through molecular paternity analyses of recruiting offspring and thus through those contributing to FD selection.

The results showed that models including FD mating performed better than alternative scenarios, which is in line with previous theory (Sinervo et al. 2007) and experimental evidence (San-Jose et al. 2014). Yearling allele frequencies were of higher importance than adult allele frequencies (large *x*), showing that intra-sexual competition among mature males could not explain the observed sexual selection pattern since in that case we would have expected very low values for *x* (ideally zero). Reproductive success of males was instead best explained when the models took into account current yearling morph frequencies as well as the adult color morph frequency, and thus the adult color morph frequency experienced by the offspring during maturation. This is in line with interpretations that intersexual selection may operate based on context-dependent (plastic) female choice, where the mating success of males varies based on the prevailing color morph frequency that will also determine offspring survival (San-Jose et al. 2014; Sinervo et al. 2007). When individual fitness depends on the local social environment (Bleay et al. 2007), context-dependent mate choice allows adjusting the reproductive behavior in order to improve fitness in each environment (Shuster and Wade 1991). Such plastic reproductive strategies confer an

advantage in the presence of environmental changes, and they constitute a paramount component of species persistence (Ghalambor et al. 2007; Shuster and Wade 2003).

Habitat humidity was an important determinant of male competitiveness and the observed patterns of sexual selection, suggesting that environmental factors can affect the maintenance of genetic variation. Habitat humidity interactively affected the color allele competitiveness and all models only including additive effects (where the effect of humidity is the same for all morphs) performed badly. The observed interactive effects might contribute to explaining why RPS orbits are irregular and deviate from the trajectories predicted by theory (Sinervo and Lively 1996). Moreover, since the climatic conditions of close populations are generally highly auto-correlated, the detected interactive effects might also explain why orbits of close populations are synchronous (Sinervo et al. 2007).

Habitat humidity may also affect RPS dynamics beyond its direct effect on sexual selection. It has been shown that habitat humidity affects growth rate (chapter I) and therefore body size—a trait that in many species, including *Z. vivipara* (Bauwens and Verheyen 1985), is closely linked with the timing of sexual maturation. Reduced yearling growth in drier habitats (Lorenzon et al. 1999; chapter I) increases the time to maturation, which will lead to longer frequency cycles (Sinervo et al. 2007). This is consistent with observations from high altitude populations, where RPS cycles are longer (Sinervo et al. 2007). Similarly, higher humidity increases juvenile survival (Marquis et al. 2008), and humidity-induced survival differences among morphs (chapter I) may indirectly affect RPS dynamics. Additional results point to differences in ecological performance among morphs in alternative humidity environments (e.g., chapter I; Sinervo et al. 2007), with the potential to affect RPS dynamics. All these effects could in principle explain deviations from a perfect RPS orbit, by increasing or decreasing the magnitude of the color morph frequency change and the speed of the frequency cycles. Morph specific ecological performances may also contribute to the existence of geographic variation in morph frequencies and they may affect the stability of the polymorphism at local scales (McLean and Stuart-Fox 2014), stressing the importance of the local polymorphic configuration (i.e., morph composition and frequency) for population dynamics and evolution (Corl et al. 2010).

The above suggests that the time to reach adult body size could have an impact on RPS cycles. Our model was not directly testing such delayed effects,

but it was able to investigate whether body size or body condition have a more immediate effect on the current sexual selection. This was, perhaps surprisingly, not supported: there was little support for any of the models in which male traits different from color morph (e.g., body condition, body size) affected male competitiveness (Table 4.2), suggesting that these traits are of reduced importance for sexual selection.

In conclusion, our results provide important experimental evidence that negative FDS operates in *Z. vivipara* and can thus potentially drive the observed RPS cycles. The results were in line with predictions of RPS theory and additionally support the hypothesis that context-dependent female mate choice, and not intra-sexual competition, imposes the observed negative FD sexual selection (San-Jose et al. 2014; Sinervo et al. 2007). Genetic polymorphisms are widespread in nature, and FD sexual selection is one of the main processes that can be responsible for their maintenance (Kokko et al. 2007). Negative FDS was affected by abiotic factors of the local environment, showing that the persistence and the evolution of polymorphisms depend on habitat conditions, since these alter the competitive environment. These results could potentially contribute to explaining why orbits of frequency cycles deviate from the regular trajectories predicted by theoretic models (Sinervo and Lively 1996), as well as why orbits of close populations are synchronous. The detected mechanisms might further generate geographic variation across a species' range, and/or population divergence with potential evolutionary consequences (e.g., speciation; McLean and Stuart-Fox 2014), they may affect the maintenance of polymorphisms, and they render populations vulnerable to environmental change, including climatic change. This shows that ecological and evolutionary processes are intertwined, bringing closer together population ecology, population genetics, and evolutionary biology (Saccheri and Hanski 2006).

Acknowledgements. We thank M. Peñalver-Alcázar and two students, L. Ros Vicente and A. M. Prieto, for assistance in the field; S. Biollay for laboratory work; L. M. San-Jose for providing background knowledge, and the Australian National University (ANU) for hosting C.R.D. while part of this research was developed. C.R.D. was supported by the Spanish Ministry of Education (FPU program), grant number AP2009-0350, and a stay in a foreign institution grant (2014, ANU). Project funds were provided by the Spanish Ministry of Education and Science (CGL2008-01522 and CGL2012-32459 to P.S.F), the Swiss National Science Foundation (PPOOP3_128375, PP00P3_152929/1 to P.S.F), and the Australian Research Council (to H.K). The capture and handling of lizards was conducted under the license provided by the Gobierno de Aragón (Ref: LC/ehv 24/2010/105 & 106) and

Gobierno de Navarra. The conducted study complies with current Spanish laws and with ASAB/ABS Guidelines for the Treatment of Animals in Behavioral Research. The authors declare no conflict of interest.

REFERENCES

Alonzo, S. H., and B. Sinervo. 2001. Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard, *Uta stansburiana*. Behavioral Ecology and Sociobiology 49:176-186.

Andersson, M. 1994, Sexual selection. Princeton, New Jersey, Princeton University Press.

Arribas, O. J. 2009. Morphological variability of the Cantabro-Pyrenean populations of *Zootoca vivipara* (Jacquin, 1787) with description of a new subspecies (Squamata: Sauria: Lacertidae). Herpetozoa 21:123-146.

Avery, R. A. 1975a. Age-structure and longevity of Common lizard (*Lacerta vivipara*) populations. Journal of Zoology 176:555-558.

Ayala, F. J., and C. A. Campbell. 1974. Frequency-Dependent Selection. Annual Review of Ecology and Systematics 5:115-138.

Bauwens, D., and R. F. Verheyen. 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. Journal of Herpetology 19:353-364.

Bleay, C., T. Comendant, and B. Sinervo. 2007. An experimental test of frequency-dependent selection on male mating strategy in the field. Proceedings of the Royal Society B-Biological Sciences 274:2019-2025.

Bleu, J., J.-F. Le Galliard, S. Meylan, M. Massot, and P. S. Fitze. 2011a. Mating does not influence reproductive investment, in a viviparous lizard. Journal of Experimental Zoology Part A: Ecological Genetics and Physiology 315:458-464.

Boudjemadi, K., O. Martin, J. C. Simon, and A. Estoup. 1999. Development and cross-species comparison of microsatellite markers in two lizard species, *Lacerta vivipara* and *Podarcis muralis*. Molecular Ecology 8:518-520.

Breedveld, M. C., and P. S. Fitze. 2015. A matter of time: delayed mate encounter postpones mating window initiation and reduces the strength of female choosiness. Behavioral Ecology and Sociobiology 69:533-541.

Burnham, K. P., and D. R. Anderson. 2002, Model selection and multimodel inference: A practical information-theoretical approach. New York, Springer-Verlag.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23-35.

Corl, A., A. R. Davis, S. R. Kuchta, and B. Sinervo. 2010. Selective loss of polymorphic mating types is associated with rapid phenotypic evolution during morphic speciation. Proceedings of the National Academy of Sciences of the United States of America 107:4254-4259.

Darwin, C. 1871, The Descent of Man, and Selection in Relation to Sex. London, Murray.

Fisher, R. A. 1930, The genetical theory of Natural Selection. Oxford, Clarendom Press.

Fitze, P. S., J. Cote, and J. Clobert. 2010. Mating order-dependent female mate choice in the poligynandrous common lizard *Lacerta vivipara*. Oecologia 162:331-341.

Fitze, P. S., J. Cote, J. P. Martínez-Rica, and J. Clobert. 2008. Determinants of male fitness: disentangling intra- and inter-sexual selection. Journal of Evolutionary Biology 21:246-255.

Fitze, P. S., V. González Jimena, L. M. San-Jose, B. Heulin, and B. Sinervo. 2014. Frequency-dependent sexual selection with respect to offspring fitness returns is consistent with predictions from rock-paper-scissors dynamics in the European common lizard. Frontiers in Ecology and Evolution 2:77.

Fitze, P. S., and J.-F. Le Galliard. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. Ecology Letters 11:432-439.

Fitze, P. S., J.-F. Le Galliard, P. Federici, M. Richard, and J. Clobert. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. Evolution 59:2451-2459.

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: Ecology and evolution. Reviews in Fish Biology and Fisheries 6:379-416.

Ghalambor, C. K., J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21:394-407.

Grafen, A. 1990. Biological signals as handicaps. Journal of Theoretical Biology 144:517-546.

Grenot, C., and B. Heulin. 1990. Sur la plasticité ecophysiologique du lézard vivipare, *Lacerta vivipara* (*Reptilia, Lacertidae*). Bulletin de la Societe Herpetologique de France 54:1-22.

Grenot, C., B. Heulin, T. Pilorge, M. Khodadoost, A. Ortega, and Y. P. Mou. 1987. Water budget in some populations of the European common lizard, *Lacerta vivipara* Jacquin. Functional Ecology 1:131-138.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology & Evolution 11:92-98.

Heulin, B. 1988. Observations sur l'organisation de la reproduction et sur les comportements sexuels et agonistiques chez *Lacerta vivipara*. Vie Milieu 38.

Heulin, B., K. Osenegg-Leconte, and D. Michel. 1997. Demography of a bimodal reproductive species of lizard (*Lacerta vivipara*): Survival and density characteristics of oviparous populations. Herpetologica 53:432-444.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19:101-108.

Kirkpatrick, M. 1982. Sexual Selection and the Evolution of Female Choice. Evolution 36:1-12.

Kokko, H., S. C. Griffith, and S. R. Pryke. 2014. The hawk-dove game in a sexually reproducing species explains a

colourful polymorphism of an endangered bird. Proceedings of the Royal Society of London Series B-Biological Sciences 281:20141794.

Kokko, H., M. D. Jennions, and A. Houde. 2007. Evolution of frequency-dependent mate choice: keeping up with fashion trends. Proceedings of the Royal Society of London Series B-Biological Sciences 274:1317-1324.

Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. Philosophical Transactions of the Royal Society B: Biological Sciences 361:319-334.

Laloi, D., M. Richard, J. Lecomte, M. Massot, and J. Clobert. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellite markers. Molecular Ecology 13:719-723.

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. Proceedings of the National Academy of Sciences 78:3721-3725.

Le Galliard, J.-F., O. Marquis, and M. Massot. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. Journal of Animal Ecology 79:1296-1307.

Lorenzon, P., J. Clobert, and M. Massot. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. Evolution 55:392-404.

Lorenzon, P., J. Clobert, A. Oppliger, and H. John-Alder. 1999. Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). Oecologia 118:423-430.

Marquis, O., M. Massot, and J.-F. Le Galliard. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. Ecology 89:2575-2583.

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639-655.

Mayer, S. S., and D. Charlesworth. 1991. Cryptic dioecy in flowering plants. Trends in Ecology & Evolution 6:320-325.

McLean, C. A., and D. Stuart-Fox. 2014. Geographic variation in animal colour polymorphisms and its role in speciation. Biological reviews of the Cambridge Philosophical Society 89:860-873.

Neff, B. D., and E. I. Svensson. 2013. Polyandry and alternative mating tactics. Philosophical Transactions of the Royal Society B: Biological Sciences 368.

Pilorge, T., and J. Castanet. 1981. Age determination in a wild population of the European viviparous lizard (*Lacerta vivipara*, Jacquin, 1787). Acta Oecologica-Oecologia Generalis 2:3-16.

Richard, M., J. Lecomte, M. de Fraipont, and J. Clobert. 2005. Age-specific mating strategies and reproductive senescence. Molecular Ecology 14:3147-3155.

Roig, J. M., M. A. Carretero, and G. A. Llorente. 2000. Reproductive cycle in a Pyrenean oviparous population of the common lizard (*Zootoca vivipara*).

Netherlands Journal of Zoology 50:15-27.

Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. Biological Reviews 79:815-848.

Saccheri, I., and I. Hanski. 2006. Natural selection and population dynamics. Trends in Ecology & Evolution 21:341-347.

San-Jose, L. M., M. Peñalver-Alcázar, B. Milá, V. Gonzalez-Jimena, and P. S. Fitze. 2014. Cumulative frequency-dependent selective episodes allow for rapid morph cycles and rock-paper-scissors dynamics in species with overlapping generations. Proceedings of the Royal Society B: Biological Sciences 281:20140976.

Shuster, S. M., and M. J. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. Nature 350:608-610.

—. 2003, Mating systems and strategies. Princeton, NJ., Princeton University Press.

Sinervo, B., and R. Calsbeek. 2006. The developmental, physiological, neural, and genetical causes and consequences of frequency-dependent selection in the wild. Annual Review of Ecology Evolution and Systematics 37:581-610.

Sinervo, B., A. Chaine, J. Clobert, R. Calsbeek, L. Hazard, L. Lancaster, A. G. McAdam et al. 2006. Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. Proceedings of the National Academy of Sciences of the United States of America 103:7372-7377.

Sinervo, B., B. Heulin, Y. Surget-Groba, J. Clobert, D. B. Miles, A. Corl, A. Chaine et al. 2007. Models of density-dependent genic selection and a new rock-paper-scissors social system. American Naturalist 170:663–680.

Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380:240-243.

Sorci, G., J. Clobert, and S. Belichon. 1996a. Phenotypic plasticity of growth and survival in the common lizard *Lacerta vivipara*. Journal of Animal Ecology 65:781-790.

Sorci, G., J. Clobert, and Y. Michalakis. 1996b. Cost of reproduction and cost of parasitism in the common lizard, Lacerta vivipara. Oikos 76:121-130.

Strijbosch, H., and R. C. M. Creemers. 1988. Comparative demography of sympratic populations of *Lacerta vivipara* and *Lacerta agilils*. Oecologia 76:20-26.

Tolle, A. E., and W. E. Wagner. 2011. Costly signals in a field cricket can indicate high- or low-quality direct benefits depending upon the environment. Evolution 65:283-294.

Werren, J. H., and E. L. Charnov. 1978. Facultative sex-ratios and population dynamics. Nature 272:349-350.

SUPPLEMENTARY MATERIAL

Table S4.1: Congruency of a) the frequency-dependency modeled by Sinervo et al. (Table 4.1; 2007), and b) the FD modeled in this study. In a) a value of 1 implies no effect of the common color allele on the focal allele ("immunity"); values 'c' or 'k' < 1 imply a negative impact, and 0 denotes "elimination" of the focal allele by the common color allele, according to the authors.

	Common adult male color allele		
	o	*w*	*y*
Juvenile allele payoff			
a) Sinervo et al. 2007			
o	$c < 1$	1	1
w	0	1	1
y	1	0	$k < 1$
b) this study			
o	α_o	α_w	α_y
w	γ_o	γ_w	γ_y
y	β_o	β_w	β_y

Table S4.2: Parameter values obtained for each model described in Table 4.1.

		Model	FPIH	FSIH	FPI	FAI	FSH
		K	9	8	6	9	9
Estimated parameters	Orange	α_b	-56.24	9.85	1.14	0.24	-1.05
		α_o (l_1)	110.16	6.59	22.60	7.88	-66.49
		α_y (l_2)	0	7.07	0	-428.28	-66.06
		α_w(l_3)	0	0	0	0	-72.98
	Yellow	β_b	-15.74	3.68	17.93	6.06	-11.52
		β_o (l_3)	0	0	0	0	-72.98
		β_y(l_1)	-82.82	6.59	-19.01	-437.80	-66.49
		β_w(l_2)/(l_4)	-5.44	7.07	-4.14	0.80	-66.06
	White	γ_b	-26.65	11.64	9.19	0.34	0.74
		γ_o(l_2)/ (l_4)	-5.44	7.07	-4.14	116.40	-66.06
		γ_y(l_3)	0	0	0	0	-72.98
		γ_w(l_1)	0	6.59	0	-960.63	-66.49
	Humidity	α_h	-0.89	-5.40			2.61
		β_h	43.04	0.05			12.26
		γ_h	1.16	-11.83			-4.23
	Body condition	α_B					
		β_B					
		γ_B					
	SVL	α_v					
		β_v					
		γ_v					

Table S4.2 (Continuation): Parameter values obtained for each model described in Table 4.1.

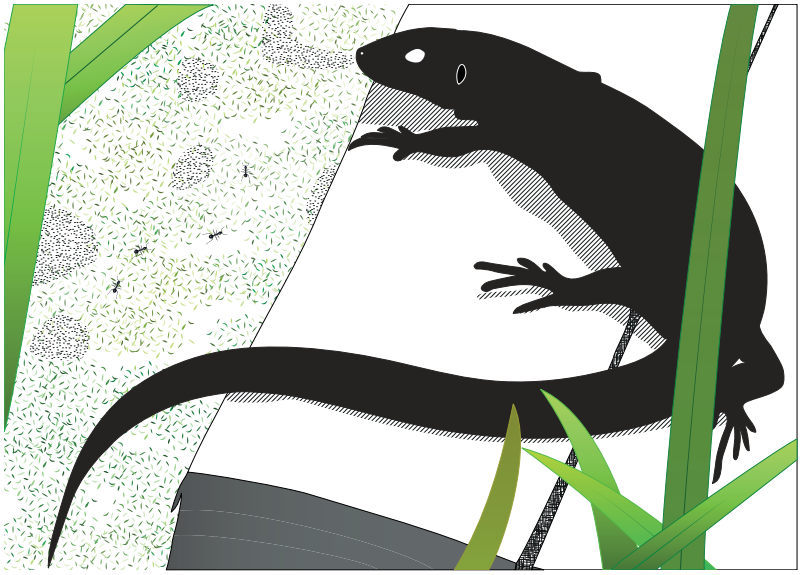
		Model	FSIHV	FSIHB	nRH	nRHB	FSI
		K	11	11	6	9	5
Estimated parameters	Orange	α_b	7.93	0.93	101.10	0.86	1.73
		α_o (l_1)	8.02	-10.24			-14.32
		α_y (l_2)	8.64	-11.19			-4.31
		α_w(l_3)	0	0			0
	Yellow	β_b	-10.24	-5.16	69.37	-2.47	0.18
		β_o (l_3)	0	0			0
		β_y(l_1)	8.02	-10.24			-14.32
		β_w(l_2)/(l_4)	8.64	-11.19			-4.31
	White	γ_b	-7.15	-1.28	101.16	0.95	-1.67
		γ_o(l_2)/ (l_4)	8.64	-11.19			-4.31
		γ_y(l_3)	0	0			0
		γ_w(l_1)	8.02	-10.24			-14.32
	Humidity	α_h	-9.24	3.94	-49.14	0.59	
		β_h	9.50	5.86	-17.94	3.31	
		γ_h	-14.69	-2.98	-51.61	-2.48	
	Body condition	α_B	0.08	1.65		0.84	
		β_B	0.06	-1.20		-0.19	
		γ_B	0.37	-0.38		0.85	
	SVL	α_v					
		β_v					
		γ_v					

Table S4.2 (Continuation): Parameter values obtained for each model described in Table 4.1.

		Model	FS	nRHV	FA	nR	R
		K	6	9	12	3	0
Estimated parameters	Orange	α_b	1.09	-0.007	-3.50	0.63	
		α_o (l_1)	256.05		-289.90		
		α_y (l_2)	266.06		-445.40		
		α_w(l_3)	270.36		1145.10		
	Yellow	β_b	-0.45	0.003	-0.50	-0.07	
		β_o (l_3)	270.36		-294.90		
		β_y(l_1)	256.05		-452.00		
		β_w(l_2)/(l_4)	266.06		1148.80		
	White	γ_b	-2.30	0.02	2.30	-0.60	
		γ_o(l_2)/ (l_4)	266.06		-96.50		
		γ_y(l_3)	270.36		278.80		
		γ_w(l_1)	256.05		-515.00		
	Humidity	α_h		-0.01			
		β_h		3.88			
		γ_h		-1.76			
	Body condition	α_B					
		β_B					
		γ_B					
	SVL	α_v		0.07			
		β_v		-0.0004			
		γ_v		-0.07			

Chapter IV

Corticosterone mediated sexual conflict affects the strength of female mating reluctance



Cristina Romero-Diaz, Virginia Gonzalez-Jimena
& Patrick S. Fitze

ABSTRACT

According to the 'chase-away' hypothesis, costly female mate choice evolved due to sexual conflict over mating rate, while traditional hypotheses put explanations based on direct or indirect fitness benefits forward. Here we disentangle among hypotheses by experimentally increasing female mating costs by means of blood corticosterone level manipulation in female common lizards (*Zootoca vivipara*). Two females, one with increased costs and one control female, were simultaneously presented to a male and thereafter to a known or a novel male, the latter treatment allowing to detect strategies maximizing indirect fitness benefits. Females with higher corticosterone levels (Cort) were more aggressive towards males and mated less. Furthermore, small Cort females did not copulate and copulation probability of Cort, but not of control females, increased with body size. The results are consistent with the chase-away hypothesis and the evolution of female strategies that reduce mating costs. The corticosterone effects and the phylogenetic conservation of the stress response further suggest that an ample range of environmental and social factors, through their effect on glucocorticoid levels, may affect sexual conflict in a wide range of species.

Keywords: Sexual selection, female choice, stress, multiple mating, novelty, lizard, *Lacerta vivipara*.

During reproduction, different sexes usually show conflicting optimal fitness strategies, resulting in a sexual conflict whose outcome is determined by the sex-specific balance of costs and benefits of mating (Parker 1979). Assuming conventional sex-roles, paternity often requires little more than a contribution of sperm, which is energetically cheap to produce. Moreover, in many species males provide less parental care than females, and in other species paternal care is absent (Clutton-Brock and Vincent 1991; Trivers 1972). It is generally accepted that male fitness is limited by the number of potential mates and not by sperm production (Andersson 1994; Bateman 1948; Trivers 1972), potentially favoring the evolution of polygyny and explaining male preference for novel females (Kelley et al. 1999; Orrell and Jenssen 2002; Tokarz 1992). Polygyny generally leads to intrasexual competition among males for access to females, which constitutes the males' costs of reproduction (Andersson 1994; Darwin 1874). In contrast to males, females typically invest more in reproduction and their number of offspring do not proportionally increase with the number of mates (Bateman 1948), potentially explaining why females exert stronger mate choice (Andersson 1994; Trivers 1972).

Traditional hypotheses argue that costly female mate choice evolved because females may gain direct (e.g., resources) or indirect benefits by means of mate choice, the latter by choosing fathers that provide 'good genes', produce 'sexy sons' ('good genes' and 'sexy sons' hypotheses; Andersson 1994; Fisher 1930; Gavrilets and Hayashi 2005; Tokarz 1995), or by optimizing the offspring's genetic diversity (Jennions and Petrie 2000). In line with these ideas are trade-up strategies during which females first assure fertilization of their eggs and thereafter mate with a male that provides 'good genes' or produces 'sexy sons' (Fitze et al. 2010). However, the costs associated with mating and particularly with multiple mating, may jeopardize survival and fecundity (Andersson 1994). Direct costs include the time and energy used for mate discrimination and mating *per se*, as well as male coercion and harassment, which can produce injuries and death (Arnqvist and Rowe 2005; Clutton-Brock and Parker 1995; Le Galliard et al. 2008; Le Galliard et al. 2005c). Indirect costs may arise due to the transmission of sexual diseases, parasites and infections (Andersson 1994). Given the ample range of costs, it is not clear whether the benefits obtained from female mate choice may indeed compensate the arising costs (Gavrilets et al. 2001; Kirkpatrick and Barton 1997).

A more recent hypothesis, the 'chase-away' hypothesis (Holland and Rice 1998), claims that female mate choice is the result of sexual conflict over mating and that females evolved resistance against males rather than preference (e.g., Gavrilets et al. 2001). In other words, whereas males benefit from mating with multiple females, females evolved resistance against suboptimal mating attempts, in order to reduce the costs of mating (Clutton-Brock and Parker 1995; Gavrilets et al. 2001; Gavrilets and Hayashi 2005; Holland and Rice 1998; Kokko 2005; Rowe et al. 2005). Recent theoretical and mathematical work provide evidence for this hypothesis, but experimental support is only available in insects (Arnqvist and Rowe 2005; Hall et al. 2008; Perry et al. 2009; Wigby and Chapman 2004).

Here we disentangle among hypotheses by experimentally amplifying the female's mating costs and by manipulating partner novelty. We quantified treatment effects on male and female reproductive behavior and reproductive success using a vertebrate, the common lizard *Zootoca vivipara*, as a model species. The polygynandrous common lizard exhibits female mate choice and females' costs of mating include harmful interactions resulting from male harassment, forced copulas, and severe injuries (Fitze et al. 2005; Fitze

and Le Galliard 2008; Le Galliard et al. 2005c). Reported reproductive costs of females moreover include the energetic burden of fecundity and pregnancy (Bleu et al. 2011b; Le Galliard et al. 2003), increased risk of predation (Van Damme et al. 1989), and increased exposure to parasites (Meylan et al. 2013; White et al. 2011). Most of these costs result in increased corticosterone levels (Dauphin-Villemant et al. 1990; Moore and Jessop 2003; Romero 2002; Tokarz and Summers 2011). Female lizards were attributed to two groups. In one group, the mating costs were amplified by manipulating blood corticosterone levels, and the behavior and reproductive success was compared with control females. Corticosterone is a glucocorticoid involved in the stress response that has important implications on reproduction, since glucocorticoids can impair or inhibit reproductive and social activity (Moore and Miller 1984; Tokarz and Summers 2011; Wingfield et al. 1998). In many species of amphibians, reptiles, birds and small mammals, females exhibit higher levels of corticosterone than males during the breeding season (e.g., Klose et al. 2006; Romero 2002; Taylor et al. 2004) and elevated levels of corticosterone affect fecundity, clutch size, hatching success, juvenile corpulence and juvenile dispersion (De Fraipont et al. 2000b; Ganesh and Yajurvedi 2002; Meylan et al. 2002), and thus are close correlates of lifetime reproductive success. We presented pairs of females—one corticosterone treated and one control female—with a single male and tested treatment effects on multiple mating, presenting female pairs on a subsequent day either with a novel or a known male.

If females try to reduce costs by restricting mating rate (see above, Holland and Rice 1998), we predicted that females with amplified mating costs (i.e., corticosterone treated females) would exhibit lower copulation probability than control females and more reluctance to mate, and to mate multiply once fertilization is ensured. Under the traditional hypotheses, we predicted that corticosterone and control females would exhibit equal copulation probability and no differences in multiple mating patterns. In this scenario, multiple mating may be a strategy to increase mating benefits, either direct or indirect (Jennions and Petrie 2000). Indirect benefits may derive e.g., from increased viability, genetic diversity, and/or sexual attractiveness of the offspring (Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Uller and Olsson 2008). So far, evidence for indirect benefits in common lizards only points towards increased genetic quality or genetic diversity (Fitze et al. 2010;

Laloi et al. 2011). Direct benefits may include e.g., obtained sperm, nuptial gifts, parental care, and access to nesting sites. Common lizards provide no parental care, no nuptial gifts, nor do they defend or monopolize nesting sites (Peñalver-Alcázar et al. 2015), thus only direct material benefits through obtaining sperm are possible, given that sperm quantity might be an additional limiting factor for female reproduction (Ball and Parker 1997; Uller and Olsson 2005). In other words, females may try to ensure the complete fertilization of the eggs by multiple mating (Birkhead 1998; Uller and Olsson 2008). In the latter case, no differences in the probability of mating with a second male may exist among corticosterone and control females, nor among novel- and known-partner females, given that all females may need to acquire additional sperm. To discern whether females may mate multiply to obtain direct or indirect benefits, females of the novel-partner group were exposed to another two novel males, and females of the known-partner group were exposed twice to the same new male (Figure 5.1). If indirect benefits are sought, we predicted that females presented to a known male would show reduced interest. However, when presented to a new male, females of the known-partner group should show the same interest as the females of the novel-partner group, given that mating with novel partners may increase the indirect benefits of mating.

Materials and methods

Species description

The common lizard, *Zootoca vivipara*, is a small polygynandrous Lacertid (snout-to-vent length (SVL) of adults: 45-70 mm) that inhabits peat bogs and moist heathland across Eurasia (Massot et al. 1992). The species presents sexual size dimorphism, with females being longer than males (Braña 1996). In the Pyrenean populations, male lizards emerge from hibernation in February-early March, on average one month prior to the females, who emerge between late March and the beginning of April (Bauwens 1981). Mating is size assortative and takes place from the first day after female emergence onwards (Breedveld and Fitze 2015; Fitze et al. 2010). Males mainly compete for access to mate partners (Fitze and Le Galliard 2011) and can father offspring of up to 14 different females, while females give birth to offspring of up to 5 different males (Fitze et al. 2005; Laloi et al. 2004). Overall, qualitatively better/bigger males are more likely to father offspring (Fitze et al. 2008; Heulin 1988). Female lizards ovulate spontaneously in absence of mating (Bleu et al. 2011a) and can lay more than one clutch per year (Heulin et al. 1994).

Experimental procedure

In 2009, adult male and female common lizards were introduced into two separate semi-natural populations at the Instituto Pirenaico de Ecología (CSIC, Jaca, Spain), to avoid any intersexual contact. Each population (100 m^2) was enclosed with galvanized metal walls and consisted of a patch of natural vegetation, two water ponds, and four stone piles providing natural food and water as well as basking sites and shelters. Forty adult males and 40 adult females were captured in the two enclosures in March and April 2010, right after female emergence. Following capture, all lizards were individually identified, weighted to the nearest mg, and measured (SVL) to the nearest mm. During the experiment lizards were housed under standardized conditions in individual terraria (25 x 15 x 15 cm) containing a water pool and shelter. Light and heat were provided by a 40W bulb from 7 a.m. to 6 p.m. and a UV lamp from 12 a.m. to 2 p.m. Water was available *ad libitum* and all animals were fed every other day with moth larvae (*Galleria mellonella*, Pyralidae). Males and females were placed in separated shelves and all individuals were isolated from neighbors. Within sexes, individuals of the same treatment group were randomly distributed among shelves and floors (all $P > 0.05$). Since female emergence from hibernation occurs over several weeks (Breedveld and Fitze 2015; pers. obs.), we attributed them to three blocks. In each block, emerging females were captured during 10±2 days and once the number of females required for a block was collected, males were captured. All mating assays took place during April. Time from emergence and time spent in captivity did not differ for lizards among blocks (all $P > 0.56$).

Corticosterone treatment

Effects of corticosterone on mate choice and intra- and intersexual behavior were investigated by experimentally manipulating blood corticosterone levels. Females of similar SVL (average range (biggest-smallest) = 0.7 mm; minimum = 0 mm; and maximum = 2 mm) and body condition (average range (biggest-smallest) = 0.35; minimum = 0.04; and maximum = 0.67) were paired. One female of the pair was randomly attributed to a corticosterone group ('Cort') and the other to a control group ('Control'). There were no differences in SVL or body condition between treatment groups ($F_{1, 38} < 0.01$, $P > 0.92$). Cort females were submitted to a daily application of a dilution of 4.5 µl of commercial sesame oil mixed with corticosterone (1.5 µg of corticosterone per µl of oil; Corticosterone Sigma C2505), a dose that raises blood corticosterone levels to an average of 194.5±7.9 ng/ml and thus by 94.7%

(Gonzalez-Jimena and Fitze 2012). In female common lizards, increases of similar magnitude occur during the mating period, more precisely, from early to mid-gestation (Dauphin-Villemant et al. 1990). Control females were treated with 4.5 µl of sesame oil only. Before the beginning of the mating assays, treatments were applied twice a day (i.e., at 6 a.m. and 6 p.m.) for four days. The duration and the magnitude of the blood corticosterone increase correspond to a corticosterone elevation observed during the acute stress response, during which animals do not shift behavior from reproduction to self-maintenance (Breuner et al. 2008). Besides the applied corticosterone treatment, the handling and conditions of confinement were exactly the same for all groups of lizards.

Set-up of mating assays

Mating assays were conducted in 2500 cm^2 escape-proof wooden boxes containing a heat rock for thermoregulation (substrate temperature 30±2°C) and two roofless cardboard refuges, allowing lizards to hide from conspecifics and be watched continuously by the observer. Natural daylight and two halogen lamps illuminated the mating boxes and surrounding dark cloth provided a standardized environment. The day before use, all boxes and heat rocks were cleaned with water-diluted bleach.

Each block was subjected to two mating trials: 'Trial A' followed by 'Trial B'. Both trials consisted of two sets of mating assays carried out on consecutive days (namely 'day 1'/'day 2'), hereafter referred to as 'day of presentation'. Female pairs (one Cort, one Control) thus had the opportunity to copulate on four consecutive days. On each day they were presented with a single male (Figure 5.1). In each trial, half of the female pairs were presented twice with the same male (the known-partner group, 'KP' henceforth) or with two different males (the novel-partner group, 'NP'). The two types of presentation are hereafter referred to as 'partner novelty'. Each male was presented to two female pairs and either used in Trial A or Trial B, while female pairs were used in both trials (Figure 5.1). Consequently, females and males had the opportunity to mate with 2 or 4 different partners, in the KP or the NP group, respectively.

The within trial design allowed testing if corticosterone and partner novelty affect 1) the probability of mating and 2) the likelihood of mating with multiple partners. Trial B was conducted to control for effects produced by potential sperm limitation (i.e., bet-hedging against insufficient sperm quantities), and in the case of its existence, to disentangle between direct and indirect benefits derived from partner novelty. A female of

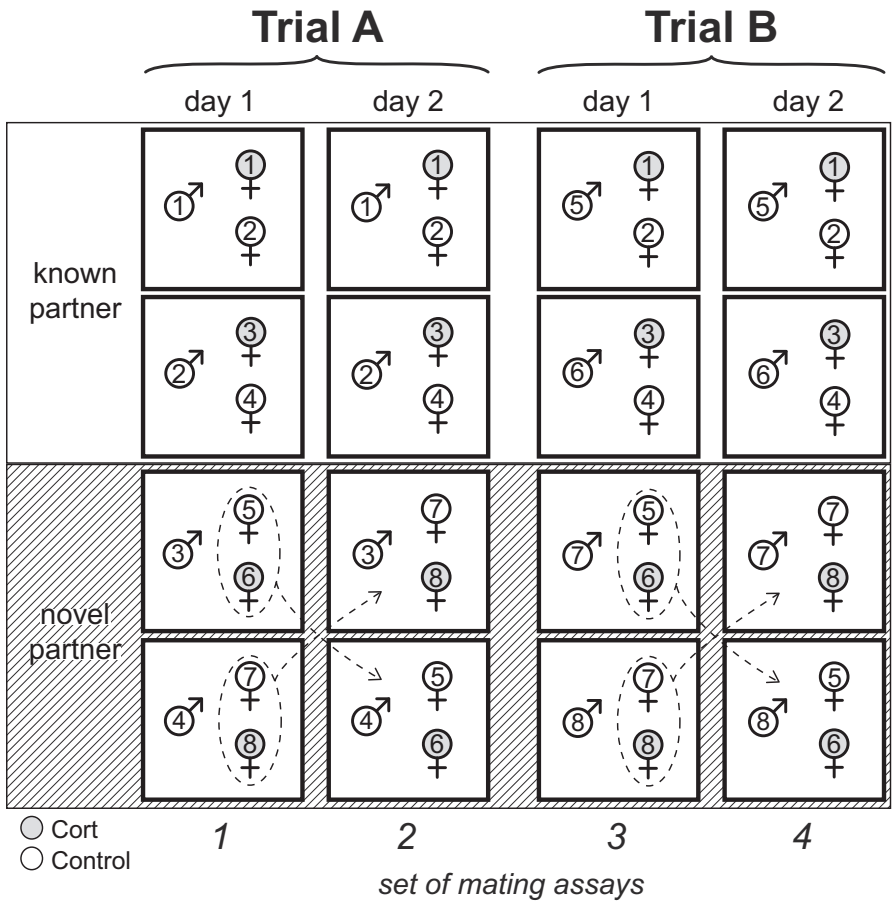


Figure 5.1 Experimental design. Each half of a block consisted of 4 sets of mating assays (rows), two trials (Trial A and Trial B, see columns), and a total of 16 mating assays. A full block consisted of twice the here shown mating assays, thus 8 sets of mating assays and 32 mating assays in total. In each mating assay one Cort (●) and one Control (○) female, were presented with one male. Half of the female pairs were presented with the same partner on two consecutive days, a.k.a. the known-partner group (KP), while the other half were presented with different partners, i.e., the novel-partner group (NP). Each female pair was used in two consecutive trials (A and B) following the same experimental design, while males were only used in one trial. See text for additional details.

the novel-partner group that shows equal mating interest in consecutive assays at Trial A (i.e., on day 1 and day 2) could i) not have enough sperm or ii) seek the novelty of her partner. A female of the known-partner group that loses interest at her second assay in Trial A (day 2), could i) already have enough sperm or ii) find a lack of novelty in her partner. Presenting either female with a new novel male in a subsequent set of assays (Trial B), resolves this ambiguity: if females copulate again, it is likely due to male novelty and not due to a lack of sperm (note: most

females lay clutches fathered by 1 or 2 males; (Fitze et al. 2005).

In blocks 1 and 2, two simultaneous mating assays were conducted in each of four time intervals (between 9 and 11h, 11 and 13h, 13 and 15h, and 15 and 17h), i.e., eight mating assays per day, whereas in block 3 one mating assay was conducted at each time interval, i.e., four mating assays per day. All experiments were conducted within the daily activity period described for this species (House et al. 1980) and the number of potential partners was within the natural range of multiple-partner mating revealed by paternity analyses (Laloi et al. 2004). Because in this species mating is size assortative (Heulin 1988) and there is sexual size dimorphism, pairs of females were matched with males of slightly smaller SVL (on average 4.3 mm smaller). Male and female SVL and body condition did not differ among treatments in any of the blocks (corticosterone treatment, $P > 0.9$; partner novelty, $P > 0.5$). In each mating assay, the male was introduced first into the box and the two females of a pair were thereafter released simultaneously to avoid the pre-setting of a dominance hierarchy (Aragón et al. 2006). Lizard behavior was recorded using digital camcorders (JVC Everio GZ-MG730) placed above the boxes at a standard distance. Videos were watched blind with respect to treatments and all intra- (female to female) and intersexual (female to male and *vice versa*) behavior was quantified. The following general behaviors were recorded: *N approaches*, *N tongue extrusions*, *N chases*, *N escapes*, *N bites*, *N fights* (i.e., 'rolling'), and *N appeasement displays* (tail and forelimb rapid movements; Gonzalez-Jimena and Fitze 2012), and the intersexual mating behaviors: *N pre-copulations*, average duration of *pre-copula*, and *probability of copulation* (1= successful copulation; 0= no copulation). All variables are described in detail elsewhere (Gonzalez-Jimena and Fitze 2012). The above mentioned behaviors were analyzed per time elapsed between introduction of the females into the box and the start of the copulation, in the case of pre-copulatory behaviors, and between the end of the copulation and the end of the mating assay in the case of post-copulatory behaviors. All behavioral variables (except those describing copulatory behavior) thus correspond to N behaviors per time unit.

Statistics

Data analyses were performed using JMP© (SAS Institute Inc.) and R (R Development Core Team 2012), with packages geepack (Yan 2002) and lme4 (Bates et al. 2011). Male and female intra- and intersexual interactive behavior,

before and after copula, was summarized using principal component (PC) analysis. Principal components with eigenvalues > 1 were selected and analyzed with Generalized Estimating Equations (GEE). Corticosterone treatment of the actor (when analyzing female behavior) or of the receiver (when analyzing male behavior), partner novelty, trial, and day of presentation were modeled as factors, their interactions included and subject ID was included using the *id* argument of the geeglm function to account for repeated measures. In the analyses of female behavior, the sex of the receiver was additionally included and a female's *average time spent walking* and *scratching/climbing* was added as a covariate to control for enhanced activity of Cort lizards. Moreover, actor SVL was included as a covariate in all analyses. The probability of copulation was analyzed using a binomial logistic mixed model, with corticosterone treatment, day of presentation, trial, and partner novelty as fixed factors and female SVL as a covariate. Partner novelty was nested within mating assay, which was modeled as a random factor. Average pre-copula duration was analyzed using GLMs with negative binomial error to account for overdispersion.

Initial models included all parameters and their interactions and non-significant terms were backward eliminated. Weighted GEEs were used to correct

Table 5.1 Principal components analysis of pre- ($_{fb;\ females\ before}$) and post-copulatory ($_{fa;\ females\ after}$) female intra- and intersexual behavior. Shown are component loadings for rotated components with eigenvalues ≥1. Main explanatory variables are depicted in bold.

	component loadings				
	pre-copulatory			post-copulatory	
behavior	$PC1_{fb}$	$PC2_{fb}$	$PC3_{fb}$	$PC1_{fa}$	$PC2_{fa}$
N tongue extrusions	-0.213	**0.764**	0.311	-0.149	**0.771**
N approaches	0.101	**0.755**	-0.188	-0.032	**0.816**
N escapes	**0.759**	-0.112	0.051	**0.897**	0. 199
N chases	0.425	0.418	-0.409	-0.096	-0.208
N appeasement displays	**0.739**	0.063	0.138	**0.918**	0.078
N bites	0.578	0.090	**0.605**	0.545	-0.271
N fights	0.123	-0.018	**0.738**		

high heteroscedasticity. Bonferroni-holm corrections were applied to post-hoc comparisons (Holm 1979). Two-tailed tests with significance level $P \leq 0.05$ were used throughout. Model assumptions were tested (Zuur et al. 2009) and results of minimal adequate models are shown.

RESULTS

Treatment effects on interactive behavior

Pre-copulatory female behavior

Three principal components had eigenvalues greater than 1 (Table 5.1). The first principal component ($PC1_{fb}$; 'females before' copulation) accounted for 26.88% of the variance in behavior. It described 'submissive behavior' since the number of appeasement displays and escapes loaded highest. The second principal component ($PC2_{fb}$) explained 19.42% of the variance and mainly described the number of approaches and tongue extrusions, hence 'interest', and the third component ($PC3_{fb}$) explained 14.99% of the variance and represented the number of fights and bites, hence 'aggressive behavior'.

Submissive behavior ($PC1_{fb}$)

Corticosterone treatment, partner novelty, day of presentation and trial did not significantly affect submissive behavior (Table 5.2). There was a significant interaction between sex and SVL (Table 5.2, Figure 5.2*a*). In general, females were more submissive towards males and submissive behavior towards males was negatively correlated with female SVL (χ^2_1 =14.20, $P < 0.001$), while submissive behavior towards females was not significantly correlated with female SVL (χ^2_1 = 4.30, P = 0.153). No other interactions were significant (all $P > 0.05$).

Interest ($PC2_{fb}$)

There was a significant interaction between corticosterone treatment and SVL on female interest (Table 5.2, Figure 5.2*b*). In Cort females interest increased with SVL (χ^2_1 =18.65, $P < 0.001$) while it was not size-dependent in Control females (χ^2_1 = 0.01, P = 1.000). Female interest was significantly lower during Trial B (Table 5.2), and partner novelty and day of presentation were not significant (all $P > 0.05$). There was also a significant interaction between the sex of the receiver and female SVL (Table 5.2, Figure 5.2*c*). Interest towards other females increased with female SVL (χ^2_1 = 9.44, P = 0.008) and no significant relationship existed towards males (χ^2_1 = 1.28, P = 1.000). All other interactions were not significant (all $P > 0.05$).

Aggressive behavior ($PC3_{fb}$)

There was a significant interaction between corticosterone treatment and sex (Table 5.2, Figure 5.3), showing that Cort

Table 5.2 Treatment effects on female pre- ($_{fb;\ females\ before}$) and post-copulatory ($_{fa;\ females\ after}$) submissive behavior (PC1), interest (PC2), and aggressive behavior (PC3). Shown are estimates ± SE (when significant), test statistics and *P* values of the minimal adequate model derived from GEEs. Estimates correspond to the factor level given in brackets and significance is depicted in bold.

Submissive behavior	$PC1_{fb}$			$PC1_{fa}$		
parameter	estimate±SE	$\chi^2(1)$	*P*	estimate ± SE	$\chi^2(1)$	*P*
Cort treatment					0.05	0.818
SVL	**-0.01±0.00**	**4.29**	**0.038**	**-0.10±0.03**	**9.52**	**0.002**
sex [males]	**0.94±0.32**	**8.83**	**0.003**	**0.56±0.15**	**13.86**	**<0.001**
trial					0.83	0.361
Cort treatment*trial [Control, Trial B]				**-0.74±0.35**	**4.33**	**0.037**
sex*SVL [males]	**-0.01±0.00**	**7.04**	**0.008**			
Interest	$PC2_{fb}$			$PC2_{fa}$		
Cort treatment [Control]	**2.85±1.00**	**8.13**	**0.004**	**4.13±1.80**	**5.25**	**0.022**
SVL	**0.06±0.01**	**24.75**	**<0.001**		2.18	0.139
sex [male]	**1.36±0.56**	**5.93**	**0.015**			
trial [Trial B]	**-0.15±0.06**	**5.28**	**0.021**	**-0.46±0.10**	**19.04**	**<0.001**
Cort treatment*SVL [Control]	**-0.05±0.02**	**8.80**	**0.003**	**-0.07±0.03**	**6.13**	**0.013**
sex*SVL [male]	**-0.02±0.01**	**5.72**	**0.017**			
Aggressive behavior	$PC3_{fb}$					
Cort treatment		0.49	0.484			
day of presentation [day 2]	**-0.05±0.02**	**3.98**	**0.046**			
SVL	**0.01±0.00**	**8.70**	**0.003**			
sex [male]	**0.09±0.03**	**6.45**	**0.011**			
Cort treatment*sex [Control, male]	**-0.09±0.04**	**4.83**	**0.028**			

females were more aggressive than Control females towards males (χ^2_1 = 5.07, P = 0.024), while no significant difference existed towards females (P = 0.394). Aggressive behavior was also conditioned by day of presentation (Table 5.2). On day 1, females were significantly more aggressive than on day 2. Additionally, larger females were more aggressive regardless of treatment (Table 5.2). Partner novelty, trial and the other interactions were not significant (all P >

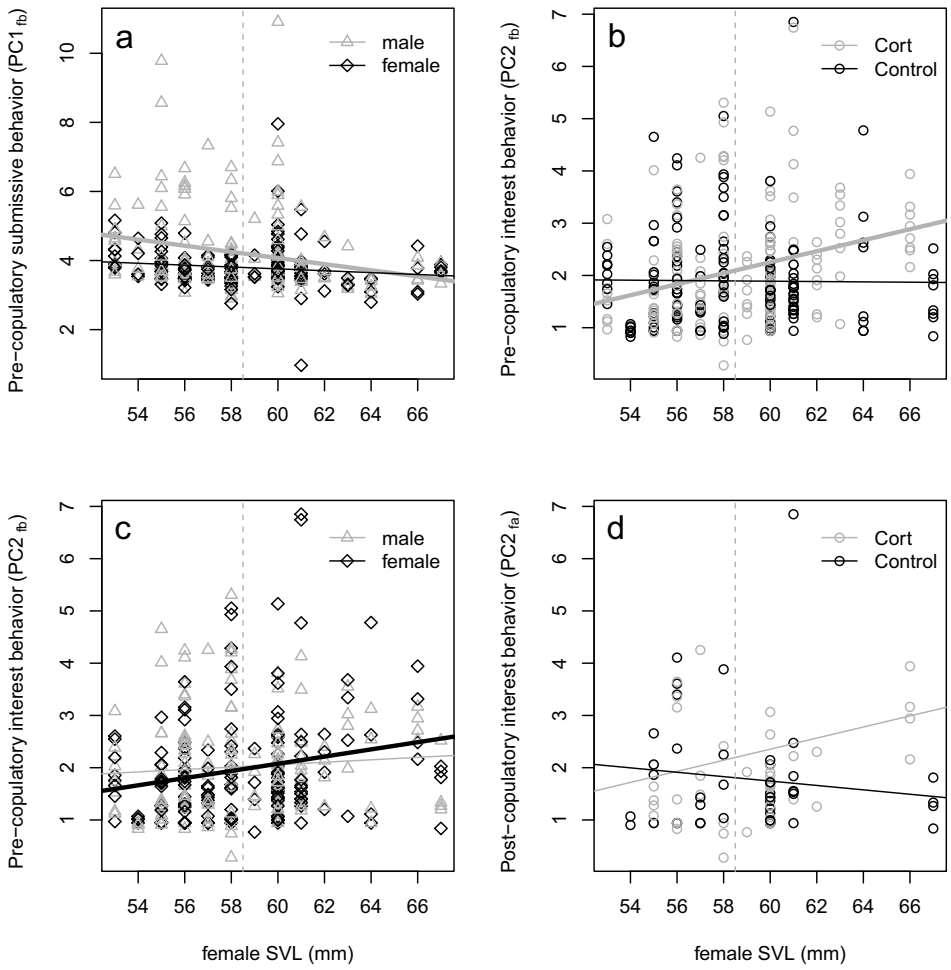


Figure 5.2 Relationship of pre- and post-copulatory female behavior and body size (SVL) depending on the sex of the receiver (a, c) or the corticosterone treatment (b, d). Shown are pre-copulatory submissive behavior ($PC1_{fb}$) and interest ($PC2_{fb}$), and post-copulatory interest ($PC2_{fa}$). The vertical dashed line depicts average female SVL and solid lines represent predictions from GEE models. Thicker lines denote significant slopes (P < 0.05).

0.05).

Post-copulatory female behavior

No fights took place after copula. Two PCs had eigenvalues >1. $PC1_{fa}$ explained 32.94% of the variance and represented submissive behavior since escapes and appeasement displays loaded highest whereas $PC2_{fa}$ accounted for 23.69% of the variance and described 'interest', because the number of approaches and tongue extrusions loaded highest (Table 5.1).

Submissive behavior ($PC1_{fa}$)

There was a significant interaction between corticosterone treatment and trial. Cort females were more submissive than Control females at Trial B (Table 5.2; individual contrast t_{83} = 2.60, P = 0.038), but not at Trial A (t_{83} = 0.23, P = 0.994). Moreover, submissive behavior showed by Cort females was not significantly different between Trial A and Trial B (t_{83} = 0.91, P = 0.750), while Control females exhibited more submissive behavior at Trial A than at Trial B (individual contrast: t_{83} = 2.65, P = 0.034). Females were more submissive against males than females, and submissive behavior was significantly and negatively correlated with female SVL (Table 5.2). Partner novelty, day of presentation and the other interactions were not significant (all P > 0.05).

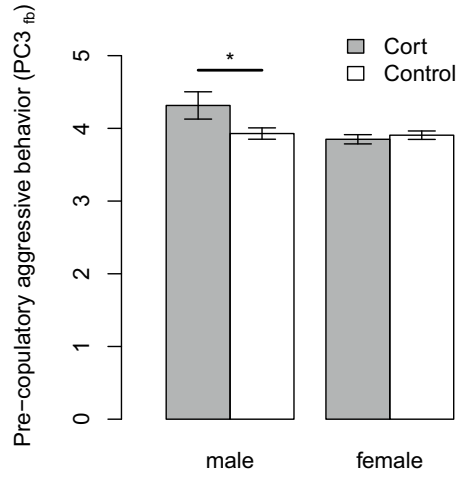


Figure 5.3 Female pre-copulatory aggressive behavior ($PC3_{fb}$) in relation to corticosterone treatment and sex of the receiver. Shown are means ± SE. Significant differences from post-hoc contrasts between groups are depicted by an asterisk (*P < 0.05).

Interest ($PC2_{fa}$)

There was a significant interaction between corticosterone treatment and SVL. Interest decreased with SVL in Control females and it increased with SVL in Cort females (Table 5.2, Figure 5.2*d*). Female interest was significantly lower during Trial B (Table 5.2) and partner novelty and day of presentation were not significant.

Pre-copulatory male behavior

Three principal components had eigenvalues >1. $PC1_{mb}$ explained 28.43% of the variance and represented 'aggressive behavior' since the number of chases and fights loaded highest. $PC2_{mb}$

explained 28.71% of the variance and escapes and appeasement displays loaded highest, representing 'submissive behavior'. $PC3_{mb}$ accounted for 17.23% of variance and described approaches and tongue extrusions, both representing 'interest' (Table 5.3).

Corticosterone treatment and partner novelty did not significantly affect male behavior (Table 5.4). Males were less aggressive ($PC1_{mb}$) on day 2 compared to day 1 (Table 5.4). Additionally, larger males were less submissive ($PC2_{mb,}$ Table 5.4). No other effects or interactions were significant (all $P > 0.05$).

Post-copulatory male behavior

No fights occurred after copulation. Three principal components had eigenvalues >1 (Table 5.3). In $PC1_{ma}$ (38.16% of variance), the number of bites, chases, and appeasement displays loaded highest, representing 'aggressive behavior'. $PC2_{ma}$ (28.95% of variance) described interest, because approaches and tongue extrusions loaded highest, whereas in $PC3_{ma}$ (18.38%) only escapes loaded high, which corresponded to 'submissive behavior'.

Males showed no significant differences in post-copulatory behavior towards Cort or Control females (Table 5.4). Male interest was significantly affected by an interaction between partner novelty and day of presentation (Table 5.4; Figure 5.4). Males exhibited

Table 5.3 Principal component analysis of pre- ($_{mb;\ males\ before}$) and post-copulatroy ($_{ma;\ males\ after}$) male intersexual behavior. Shown are component loadings for rotated components with eigenvalues ≥1. Main explanatory variables are depicted in bold.

	component loadings					
	pre-copulatory			post-copulatory		
behavior	$PC1_{mb}$	$PC2_{mb}$	$PC3_{mb}$	$PC1_{ma}$	$PC2_{ma}$	$PC3_{ma}$
N tongue extrusions	0.057	-0.193	**0.827**	-0.028	**0.948**	-0.086
N approaches	0.107	0.243	**0.785**	-0.050	**0.948**	0.072
N escapes	0.035	**0.819**	-0.013	-0.022	0.011	**0.927**
N chases	**0.904**	-0.069	0.045	**0.961**	-0.054	0.121
N appeasement displays	-0.020	**0.805**	0.040	**0.911**	-0.011	-0.146
N bites	0.518	0.097	0.085	**0.621**	-0.065	0.524
N fights	**0.891**	-0.051	0.042			

more interest in the NP compared to the KP group on day 2 (χ^2_1 = 6.56, P = 0.021), but not on day 1 (χ^2_1 = 1.97, P = 0.160). Moreover, males of the KP group showed significantly more interest on day 1 compared to day 2 (χ^2_1 = 12.57, P < 0.001). Interest was also affected by the interaction between partner novelty and SVL (Table 5.4), it significantly increased with male SVL in the KP (χ^2_1 = 5.69, P = 0.034), but not in the NP group (P > 0.111).

There was a significant interaction between day of presentation and male SVL in all male behaviors (Table 5.4). On day 2, more aggressive, more submissive

Table 5.4 Treatment effects on pre- ($_{mb;\ males\ before}$) and post-copulatory ($_{ma;\ males\ after}$) aggressive behavior ($PC1_{mb}$, $PC1_{ma}$), submissive behavior ($PC2_{mb}$, $PC3_{ma}$), and interest ($PC3_{mb}$, $PC2_{ma}$) of males. Shown are estimates ± SE (when significant), test statistics and P values of the minimal adequate model derived from GEEs. Estimates correspond to the factor level given in brackets and significance is depicted in bold.

Submissive behavior	$PC2_{mb}$			$PC3_{ma}$		
parameter	estimate ± SE	$\chi^2(1)$	P	estimate ± SE	$\chi^2(1)$	P
day of presentation [day 2]				**19.31±2.53**	**14.16**	**<0.001**
SVL	**-0.01±0.00**	**4.88**	**0.027**		0.20	0.656
day of presentation*SVL [day 2]				**-0.35±0.09**	**14.21**	**<0.001**
Interest	$PC3_{mb}$			$PC2_{ma}$		
partner novelty [KP]				**-12.97±5.10**	**6.46**	**0.011**
day of presentation				**-14.94±4.96**	**9.08**	**0.003**
SVL				**-0.21±0.08**	**18.84**	**<0.001**
partner novelty*day of presentation [KP, day 2]				**-0.92±0.37**	**6.20**	**0.013**
partner novelty*SVL [KP]				**0.24±0.09**	**6.53**	**0.011**
day of presentation*SVL [day 2]				**0.27±0.09**	**8.66**	**0.003**
Aggressive behavior	$PC1_{mb}$			$PC1_{ma}$		
day of presentation [day 2]	**-0.34±0.14**	**6.11**	**0.013**	**15.26±4.06**	**14.08**	**<0.001**
SVL					0.48	0.489
day of presentation*SVL [day 2]				**-0.27±0.07**	**14.13**	**<0.001**

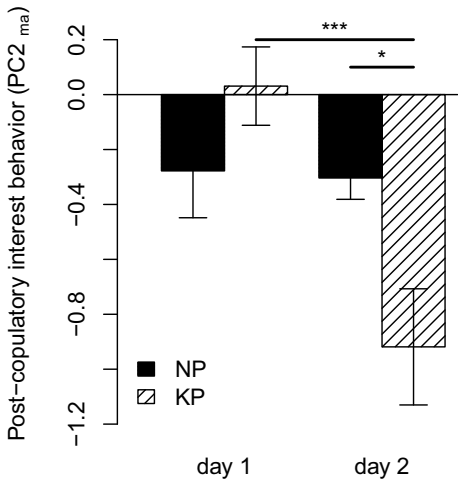


Figure 5.4 Interactive effect of partner novelty and day of presentation on male post-copulatory interest ($PC2_{ma}$). Shown are predicted means ± SE from the GEE model. Significant post-hoc contrasts between groups are depicted by an asterisk (* $P < 0.05$; *** $P < 0.001$).

and less interest behavior were exhibited, and both aggressive and submissive behaviors decreased while interest increased with increasing male body size ($PC1_{ma}$: $\chi^2_1 = 16.61$, $P < 0.001$; $PC2_{ma}$: $\chi^2_1 = 7.86$, $P = 0.010$; $PC3_{ma}$: $\chi^2_1 = 21.30$, $P < 0.001$, respectively). No size-dependent effects existed on day 1 (all $P \geq 0.084$).

Mating behavior

Average pre-copulation duration did not depend on corticosterone treatment, partner novelty, day of presentation, or trial (all $P > 0.05$). However, male SVL positively predicted pre-copulation duration ($\chi^2_1 = 6.22$, $P = 0.012$; estimate = 0.24±0.10).

Twenty-two of the 80 mating assays (27.5%) resulted in successful copulation. In none of the assays did a male copulate with more than one female. Of the 22 copulations, 17 occurred with Control (9 NP, 8 KP) and 5 with Cort (5 KP) females (Figure 5.5*a*). The probability of copulation was significantly affected by an interaction between corticosterone treatment and female SVL ($\chi^2_1 = 5.39$, $P = 0.020$). The probability of copulation increased with SVL in Cort females and it was not size-dependent in Control females (Figure 5.5*b*). Small Cort females did not copulate at all, while small females of the Control group copulated with the same probability as large females. 68.18% of the copulations occurred on day 1, and 22.73% of females mated more than once. 60% of the multiple mating females belonged to the KP and 40% to the NP group. Corticosterone treatment, partner novelty and day of presentation were not significant (all $P > 0.05$).

DISCUSSION

Two sets of competing hypotheses may explain why females are choosy. Traditional hypotheses argue that costly female mate choice evolved because females may gain direct or indirect benefits, while the chase-away hypothesis suggests that females evolved resistance, rather than preference to males (e.g.,

Gavrilets et al. 2001). The latter predicts that the costs associated with mating, and not the expected benefits, determine a female's will to mate. Here we disentangle among hypotheses by amplifying the costs in females, but not in males, and assessing its effect on mating behavior of both sexes. The level of blood corticosterone of female common lizards was manipulated right after emergence from hibernation, when females are exposed to stressors such as male harassment (leading to energetic demands and physical struggle) and reproductive investment (e.g., egg production and carrying of offspring).

As predicted by the chase-away hypothesis, mating behavior significantly differed among Cort and Control females, both before and after copulation. Cort females were significantly more aggressive towards males (Figure 5.3), they bit and fought more, being consistent with more pronounced reluctance. As a consequence, Cort females copulated significantly less than Control females (Figure 5.5*a*), which is in line with the chase-away hypothesis. Moreover, amplification of the experienced costs affected female behavior (Figure 5.2*b, d*) and reproduction in a size-dependent manner (Figure 5.5*b*). Interest increased with body size in Cort but not in Control females, suggesting that in the Cort

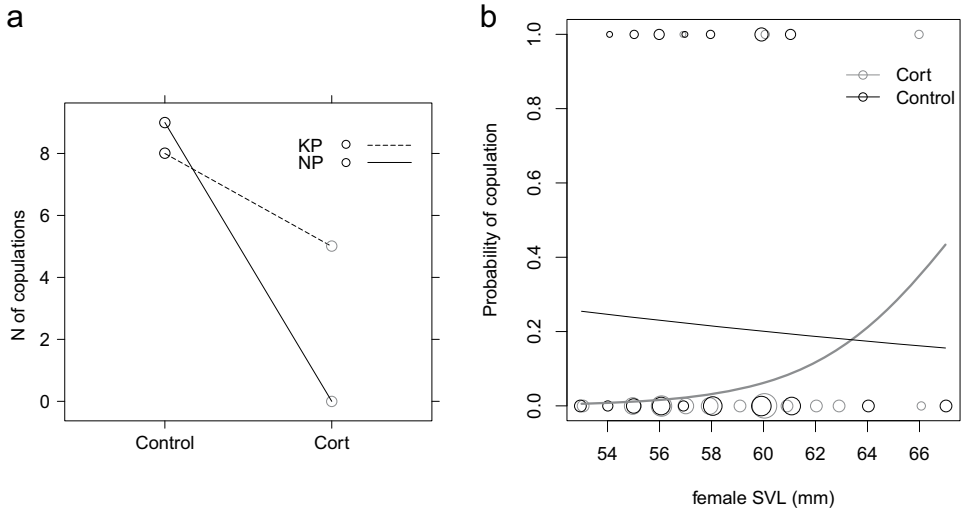


Figure 5.5 (a) Number of copulations in relation to corticosterone treatment (Cort/Control) and partner novelty (KP/NP). (b) Probability of copulation in relation to corticosterone treatment and female SVL. Model predictions for Cort (grey) and Control (black) groups are depicted with solid lines. In (b) data point size corresponds to the number of females, with the smallest dot representing $n = 1$ and the biggest dot $n = 18$.

treatment only large females could afford exhibiting increased interest. There was a similar interaction on the probability of copulation. Indeed, smaller females of the Cort group did not copulate at all, while larger females of the Cort group copulated with the same probability as Control females. This pattern cannot be attributed to differential corticosterone levels between small and large females, since basal and post-treatment corticosterone levels vary among individuals independently of female body size or corpulence (Meylan et al. 2003; Summers 1995). The observed effects on interest and copulation probability are consistent with previous experiments by Le Galliard *et al.* (2008) and Fitze *et al.* (2005) where, in populations of male-biased sex ratio (populations with higher reproductive costs to females), females exhibited reduced reproductive investment and increased number of mating partners with increased female body size, respectively. These size-dependent effects suggest that large and short females respond differently to raises in corticosterone levels. Larger females may be better able to cope with adversity and, consequently, the experienced mating costs may have a lower relative importance (e.g., Summers 1995). Also, the benefits associated with their larger size (e.g., larger clutch size; Barbault and Mou 1988) might offset the costs.

Under the chase-away hypothesis, females incurring in higher mating costs should exhibit higher reluctance to copulate in order to avoid additional mating costs, imposing direct selection on mating biases (Kokko et al. 2003; Kokko and Monaghan 2001; West-Eberhard 1983). In this study, males that successfully copulated with Cort females had on average significantly larger SVLs (an indicator of male quality) than males that copulated with Control females ($F_{1,20}$ = 5.01, P = 0.037; see also Fitze et al. 2010), which is in line with this prediction.

According to the traditional hypotheses, we predicted that females may mate multiply to gain indirect benefits. Here we found no evidence for such a strategy, since Cort females mated less than Control females and copulated on average with larger males. Moreover, partner novelty did not increase females' interest, nor the probability of copulating and there were no significant differences between treatment groups in the probability of multiple mating. Females also exhibited more interest towards females than males (Figure 5.2*c*), less interest in Trial B, and more submissive (i.e., appeasement displays, escapes) and aggressive behavior towards males than females independently of treatments, congruent with the avoidance of males and reluctance to copulations.

Males showed reduced post-copulatory interest towards KP on day 2 (Figure 5.4), an interaction that was expected since in the KP group the female pair presented on day 1 was also novel. Males also exhibited size-dependent pre-copulatory submissive behavior and post-copulatory interest. No other treatment effects existed, showing that a male's behavior towards Cort and Control females did not differ and thus male and female behavior were independent. In other words, increased aggression of Cort females towards males cannot be explained by increased interest or harassment of males towards Cort females.

The detected effects of corticosterone (i.e., of the acute stress response) on intersexual selection and female mating behavior suggest that many other intrinsic or extrinsic factors may affect a female's mating behavior and thereby the strength of sexual selection through their effects on glucocorticoid levels. For example, unpredictable extrinsic events, sources of stress, have been reported to increase corticosterone levels within minutes or hours (Wingfield et al. 1998). Such events include the appearance of predators, conspecifics, parasites, infection, and wounding, and at the population scale, parameters like population density (e.g., crowding), food-predator balance, and weather conditions (Le Galliard et al. 2008; Summers and Norman 1988; Svensson et al. 2001; Wingfield 2003). Low temperatures, storms, heavy rain, floods, low humid areas, among others have shown to trigger rapid glucocorticoid secretion (Wingfield and Kitaysky 2002) in numerous species of vertebrates (Cash and Holberton 2005; Jessop et al. 2000; Wingfield 1983; Wingfield 2003), suggesting that they may affect the cost/benefit balance and thus the opportunity and intensity of sexual selection (Berger et al. 2014; Hall et al. 2008) in a large number of organisms (Clinchy et al. 2004; Summers and Norman 1988).

In summary, here we show that increased costs during mating, simulated by manipulating blood corticosterone levels, led to higher female reluctance and thereby to stronger intersexual selection. The results are congruent with the chase-away hypothesis, which suggests that females evolved resistance to reduce the direct costs of mating. Moreover, they suggest that factors affecting glucocorticoid levels, and possibly other physiological components, may directly feedback on the strength of sexual selection. Given the phylogenetic conservation of the stress response in vertebrates, it is thus likely that in many species an ample range of extrinsic environmental and social factors affect

the intensity of sexual selection and, more generally, the strength of the sexual conflict.

Acknowledgements. CRD and VGJ were supported by the Spanish Ministry of Education (FPU program) grants number AP2009-0350 and AP2006-01678 respectively. Project funds were provided by the Spanish Ministry of Education and Science (grant numbers CGL2008-01522, CGL2012-32459 to P.S.F) and the Swiss National Science Foundation (grant numbers PPOOP3_128375, PP00P3_152929/1 to P.S.F). The handling and experimentation were conducted under licenses from the Gobierno de Aragón (LC/ehv 24/2010/105 & 106) and Navarra.

REFERENCES

Andersson, M. 1994, Sexual selection. Princeton, New Jersey, Princeton University Press.

Aragón, P., J. Clobert, and M. Massot. 2006. Individual dispersal status influences space use of conspecific residents in the common lizard, *Lacerta vivipara*. Behavioral Ecology and Sociobiology 60:430-438.

Arnqvist, G., and T. Nilsson. 2000. The evolution of polyandry: multiple mating and female fitness in insects. Animal Behaviour 60:145-164.

Arnqvist, G., and L. Rowe. 2005, Sexual conflict. Princeton, New Jersey, Princeton University Press.

Ball, M. A., and G. A. Parker. 1997. Sperm competition games: Inter- and intra-species results of a continuous external fertilization model. Journal of Theoretical Biology 186:348-355.

Barbault, R., and Y. P. Mou. 1988. Population dynamics of the common lizard, *Podarcis muralis*, in southwestern France. Herpetologica 44:38-47.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity 2:349-368.

Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes. URL http://lme4.r-forge.r-project.org/.

Bauwens, D. 1981. Survivorship during hibernation in the european common lizard, *Lacerta vivipara*. Copeia 1981:741-744.

Berger, D., K. Grieshop, M. I. Lind, J. Goenaga, A. A. Maklakov, and G. Arnqvist. 2014. Intralocus sexual conflict and environmental stress. Evolution 68:2184-2196.

Birkhead, T. R. 1998. Sperm competition in birds. Reviews of Reproduction 3:123-129.

Bleu, J., J.-F. Le Galliard, S. Meylan, M. Massot, and P. S. Fitze. 2011a. Mating does not influence reproductive investment, in a viviparous lizard. Journal of Experimental Zoology Part A: Ecological Genetics and Physiology 315:458-464.

Bleu, J., M. Massot, C. Haussy, and S. Meylan. 2011b. Experimental litter size reduction reveals costs of gestation and delayed effects on offspring in a viviparous lizard. Proceedings of the Royal Society B: Biological Sciences 279:489-498.

Braña, F. 1996. Sexual dimorphism in lacertid lizards: Male head increase vs female abdomen increase? Oikos 75:511-523.

Breedveld, M. C., and P. S. Fitze. 2015. A matter of time: delayed mate

encounter postpones mating window initiation and reduces the strength of female choosiness. Behavioral Ecology and Sociobiology 69:533-541.

Breuner, C. W., S. H. Patterson, and T. P. Hahn. 2008. In search of relationships between the acute adrenocortical response and fitness. General and Comparative Endocrinology 157:288-295.

Cash, W. B., and R. L. Holberton. 2005. Endocrine and behavioral response to a decline in habitat quality: effects of pond drying on the slider turtle, *Trachemys scripta*. Journal of Experimental Zoology Part A: Comparative Experimental Biology 303A:872-879.

Clinchy, M., L. Zanette, R. Boonstra, J. C. Wingfield, and J. N. M. Smith. 2004. Balancing food and predator pressure induces chronic stress in songbirds. Proceedings of the Royal Society B: Biological Sciences 271:2473-2479.

Clutton-Brock, T. H., and G. A. Parker. 1995. Sexual coercion in animal societies. Animal Behaviour 49:1345-1365.

Clutton-Brock, T. H., and A. C. J. Vincent. 1991. Sexual selection and the potential reproductive rates of males and females. Nature 351:58-60.

Darwin, C. 1874, The descent of man, and selection in relation to sex. London, Murray.

Dauphin-Villemant, C., F. Leboulenger, F. Xavier, and H. Vaudry. 1990. Adrenal activity in the female lizard *Lacerta vivipara* Jacquin associated with breeding activities. General and Comparative Endocrinology 78:399-413.

De Fraipont, M., J. Clobert, H. John, and S. Alder. 2000b. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. Journal of Animal Ecology 69:404-413.

Fisher, R. A. 1930, The genetical theory of Natural Selection. Oxford, Clarendom Press.

Fitze, P. S., J. Cote, and J. Clobert. 2010. Mating order-dependent female mate choice in the poligynandrous common lizard *Lacerta vivipara*. Oecologia 162:331-341.

Fitze, P. S., J. Cote, J. P. Martínez-Rica, and J. Clobert. 2008. Determinants of male fitness: disentangling intra- and inter-sexual selection. Journal of Evolutionary Biology 21:246-255.

Fitze, P. S., and J.-F. Le Galliard. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. Ecology Letters 11:432-439.

Fitze, P. S., and J.-F. Le Galliard. 2011. Inconsistency between different measures of sexual selection. American Naturalist 178:256-268.

Fitze, P. S., J.-F. Le Galliard, P. Federici, M. Richard, and J. Clobert. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. Evolution 59:2451-2459.

Ganesh, C. B., and H. N. Yajurvedi. 2002. Stress inhibits seasonal and FSH-induced ovarian recrudescence in the lizard, *Mabuya carinata*. Journal of Experimental Zoology 292:640-648.

Gavrilets, S., G. Arnqvist, and U. Friberg. 2001. The evolution of female mate

choice by sexual conflict. Proceedings of the Royal Society B: Biological Sciences 268:531-539.

Gavrilets, S., and T. I. Hayashi. 2005. Speciation and sexual conflict. Evolutionary Ecology 19:167-198.

Gonzalez-Jimena, V., and P. S. Fitze. 2012. Blood corticosterone levels and intersexual selection games: best-of-bad-job strategies of male common lizards. Behavioral Ecology and Sociobiology 66:305-315.

Hall, M. D., L. F. Bussiere, J. Hunt, and R. Brooks. 2008. Experimental evidence that sexual conflict influences the opportunity, form and intensity of sexual selection. Evolution 62:2305-2315.

Heulin, B. 1988. Observations sur l'organisation de la reproduction et sur les comportements sexuels et agonistiques chez *Lacerta vivipara*. Vie Milieu 38.

Heulin, B., K. Osenegg, and D. Michel. 1994. Survie et incubation des oeufs dans deux populations ovipares de *Lacerta vivipara*. Amphibia-Reptilia 15:199-219.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65-70.

Holland, B., and W. R. Rice. 1998. Perspective: Chase-away sexual selection: Antagonistic seduction versus resistance. Evolution 52:1-7.

House, S. M., P. J. Taylor, and I. F. Spellerberg. 1980. Patterns of daily behaviour in two lizard species *Lacerta agilis* L. and *Lacerta vivipara* Jacquin. Oecologia 44:396-402.

Jennions, M. D., and M. Petrie. 2000. Why do females mate multiply? A review of the genetic benefits. Biological Reviews 75:21-64.

Jessop, T. S., M. Hamann, M. A. Read, and C. J. Limpus. 2000. Evidence for a hormonal tactic maximizing green turtle reproduction in response to a pervasive ecological stressor. General and Comparative Endocrinology 118:407-417.

Kelley, J. L., J. A. Graves, and A. E. Magurran. 1999. Familiarity breeds contempt in guppies. Nature 401:661-662.

Kirkpatrick, M., and N. H. Barton. 1997. The strength of indirect selection on female mating preferences. Proceedings of the National Academy of Sciences of the United States of America 94:1282-1286.

Klose, S. M., C. L. Smith, A. J. Denzel, and E. K. V. Kalko. 2006. Reproduction elevates the corticosterone stress response in common fruit bats. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 192:341-350.

Kokko, H. 2005. Treat 'em mean, keep 'em (sometimes) keen: evolution of female preferences for dominant and coercive males. Evolutionary Ecology 19:123-135.

Kokko, H., R. Brooks, M. D. Jennions, and J. Morley. 2003. The evolution of mate choice and mating biases. Proceedings of the Royal Society B: Biological Sciences 270:653-664.

Kokko, H., and P. Monaghan. 2001. Predicting the direction of sexual selection. Ecology Letters 4:159-165.

Laloi, D., C. Eizaguirre, P. Fédérici, and M. Massot. 2011. Female choice for heterozygous mates changes along successive matings in a lizard. Behavioural Processes 88:149-154.

Laloi, D., M. Richard, J. Lecomte, M. Massot, and J. Clobert. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellite markers. Molecular Ecology 13:719-723.

Le Galliard, J.-F., J. Cote, and P. S. Fitze. 2008. Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. Ecology 89:56-64.

Le Galliard, J.-F., P. S. Fitze, R. Ferrière, and J. Clobert. 2005c. Sex ratio bias, male aggression, and population collapse in lizards. Proceedings of the National Academy of Sciences of the United States of America 102:18231–18236.

Le Galliard, J.-F., M. Le Bris, and J. Clobert. 2003. Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. Functional Ecology 17:877-885.

Massot, M., J. Clobert, T. Pilorge, J. Lecomte, and R. Barbault. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. Ecology 73:1742-1756.

Meylan, S., J. Belliure, J. Clobert, and M. de Fraipont. 2002. Stress and body condition as prenatal and postnatal determinants of dispersal in the common lizard (*Lacerta vivipara*). Hormones and Behavior 42:319-326.

Meylan, S., A. M. Dufty, and J. Clobert. 2003. The effect of transdermal corticosterone application on plasma corticosterone levels in pregnant *Lacerta vivipara*. Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology 134:497-503.

Meylan, S., M. Richard, S. Bauer, C. Haussy, and D. Miles. 2013. Costs of mounting an immune response during pregnancy in a lizard. Physiological and Biochemical Zoology 86:127-136.

Moore, F. L., and L. J. Miller. 1984. Stress-induced inhibition of sexual behavior: corticosterone inhibits courtship behaviors of a male amphibian (*Taricha granulosa*). Hormones and Behavior 18:400-410.

Moore, I. T., and T. S. Jessop. 2003. Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. Hormones and Behavior 43:39-47.

Orrell, K. S., and T. A. Jenssen. 2002. Male mate choice by the lizard *Anolis carolinensis*: a preference for novel females. Animal Behaviour 63:1091-1102.

Parker, G. A. 1979. Sexual selection and sexual conflict, Pages 123-166 *in* M. S. Blum, and N. A. Blum, eds. Sexual selection and reproductive competition in insects. New York, Academic Press.

Peñalver-Alcázar, M., C. Romero-Diaz, and P. S. Fitze. 2015. Communal egg-laying in oviparous *Zootoca vivipara louislantzi* of the Central Pyrenees. Herpetology Notes 8:4-7.

Perry, J. C., D. M. T. Sharpe, and L. Rowe. 2009. Condition-dependent female remating resistance generates sexual selection on male size in a ladybird beetle. Animal Behaviour 77:743-748.

R Development Core Team. 2012.R: A language and environment for statistical computing.R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org.

Romero, L. M. 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. General and Comparative Endocrinology 128:1-24.

Rowe, L., E. Cameron, and T. Day. 2005. Escalation, retreat, and female indifference as alternative outcomes of sexually antagonistic coevolution. American Naturalist 165:S5-S18.

Summers, C. H. 1995. Regulation of ovarian recrudescence: Different effects of corticotropin in small and large female lizards, *Anolis carolinensis*. Journal of Experimental Zoology 271:228-234.

Summers, C. H., and M. F. Norman. 1988. Chronic low humidity-stress in the lizard *Anolis carolinensis*: changes in diurnal corticosterone rhythms. Journal of Experimental Zoology 247:271-278.

Svensson, E., B. Sinervo, and T. Comendant. 2001. Density-dependent competition and selection on immune function in genetic lizard morphs. Proceedings of the National Academy of Sciences of the United States of America 98:12561-12565.

Taylor, E. N., D. F. DeNardo, and D. H. Jennings. 2004. Seasonal steroid hormone levels and their relation to reproduction in the western diamond-backed rattlesnake, *Crotalus atrox* (Serpentes: Viperidae). General and Comparative Endocrinology 136:328-337.

Tokarz, R. R. 1992. Male mating preference for unfamiliar females in the lizard, *Anolis sagrei*. Animal Behaviour 44:843-849.

Tokarz, R. R. 1995. Mate choice in lizards: a review. Herpetological Monographs 9:17–40.

Tokarz, R. R., and C. H. Summers. 2011. Stress and reproduction in reptiles, Pages 169-213 *in* D. O. Norris, and K. H. Lopez, eds. Hormones and Reproduction of Vertebrates, Academic Press.

Trivers, R. L. 1972. Parental investment and sexual selection, Pages 136-207 *in* B. Campbell, ed. Sexual Selection and the descent of man 1871-1971. Chicago, Aldine Publishing Company.

Uller, T., and M. Olsson. 2005. Multiple copulations in natural populations of lizards: Evidence for the fertility assurance hypothesis. Behaviour 142:45-56.

—. 2008. Multiple paternity in reptiles: Patterns and processes. Molecular Ecology 17:2566-2580.

Van Damme, R., D. Bauwens, and R. F. Verheyen. 1989. Effect of relative clutch mass on sprint speed in the lizard *Lacerta vivipara*. Journal of Herpetology 23:459-461.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology 58:155-183.

White, J., M. Richard, M. Massot, and S. Meylan. 2011. Cloacal bacterial diversity increases with multiple mates: Evidence of sexual transmission in female common lizards. PLoS ONE 6.

Wigby, S., and T. Chapman. 2004. Female resistance to male harm evolves in response to manipulation of sexual conflict. Evolution 58:1028-1037.

Wingfield, J. C. 1983. Endocrine responses to inclement weather in naturally breeding populations of white-crowned sparrows (*Zonotrichia leucophrys pugetensis*). The Auk 100:56.

—. 2003. Control of behavioural strategies for capricious environments. Animal Behaviour 66:807-815.

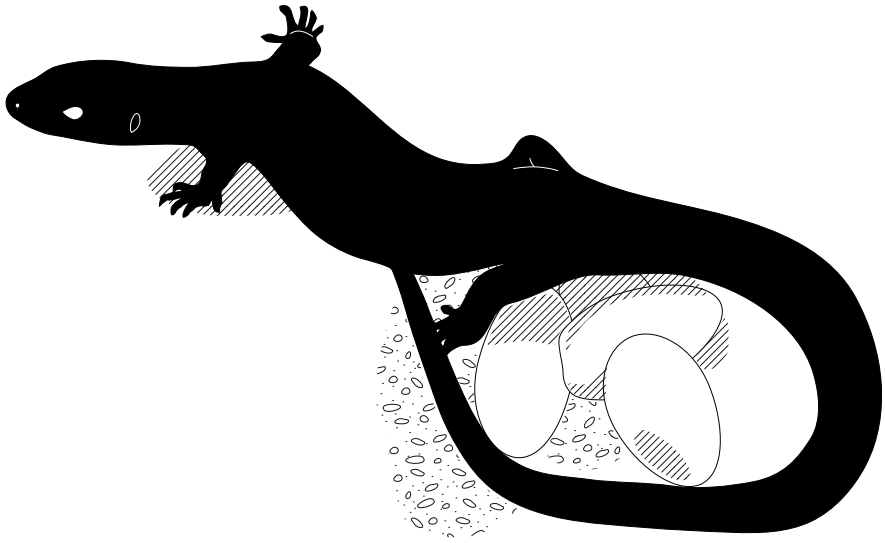
Wingfield, J. C., and A. S. Kitaysky. 2002. Endocrine responses to unpredictable environmental events: Stress or anti-stress hormones? Integrative and Comparative Biology 42:600-609.

Wingfield, J. C., D. L. Maney, C. W. Breuner, J. D. Jacobs, S. Lynn, M. Ramenofsky, and R. D. Richardson. 1998. Ecological bases of hormone-behavior interactions: The "emergency life history stage". American Zoologist 38:191-206.

Yan, J. 2002. Geepack: yet another package for generalized estimating equations. R News 2:12-14.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009, Mixed effects models and extensions in ecology with R. New York, NY, USA, Springer.

General Discussion



The preservation of biodiversity is one of the most challenging endeavors the scientific community has undertaken and huge efforts are being devoted in order to improve the efficacy of current and future species' management actions in the face of recent and upcoming environmental change. However, although there is a growing body of work that investigates the causes and mechanisms of population decline leading to the loss of biodiversity (Pacifici et al. 2015), there is an urgent need to investigate a wider range of species at a more detailed level to draw robust conclusions based on causation and in this way identify the proximate causes of climate-change related extinctions (Cahill et al. 2013; Dawson et al. 2011). This thesis had the broad aim to contribute reliable knowledge on the factors and mechanisms driving population dynamics by experimentally assessing relationships of causation between environmental change and individual life-histories.

Population dynamics and life-history evolution

Species' population dynamics are governed by changes in demographic rates (e.g., births, deaths, migration), which in turn produce changes in population size, structure, or spatial distribution over time (Benton et al. 2006). Today, it is widely recognized that the presence of density dependence is one of the necessary conditions for population regulation to occur (Turchin 1995). Nevertheless, virtually all populations are influenced by exogenous variables and population dynamics result from the interplay of density-dependent and density-independent processes (Benton et al. 2006). Consequently, it has become extremely relevant to assess how exogenous factors interact with the demographic characteristics of populations, especially since this can help improve the effectiveness of conservation measures, slowing down the loss of biodiversity.

In this thesis, we have experimentally studied the effects of exogenous and endogenous factors (and their interaction) on semi-natural populations to reveal the underlying biological mechanisms of regulation using the common lizard, *Zootoca vivipara*, as a model species. We hypothesized that environmental changes predicted by future scenarios of climate change would affect life-history traits that determine individual fitness, possibly in different ways for individuals of different stages, altering demographic rates and thus the trajectory of the population in a potentially unexpected direction. As seen in chapters I and II, several immediate effects on life-history traits resulted from the interaction between habitat humidity, morph frequency and age structure, from habitat humidity on age structure, and precipitation

(humidity) stochasticity on age structure. Both experiments suggested that mechanisms of asymmetric inter-cohort competition between the adult and younger age classes and also intra-cohort competition, at least among adults, importantly affect the dynamics of common lizard populations, confirming the key role of density-dependent processes in population regulation. A straightforward cause of competition among age classes was likely ecological (i.e., competition for resources such as food or space), since there is ample overlap in the size of prey items across ages (Avery 1966). This density-dependent effect might have stemmed from the indirect variation in resource abundance due to changes in environmental humidity (Chikoski et al. 2006; Tsiafouli et al. 2005). The main effects of humidity and their interaction with morph frequency (chapters I and III) further pointed towards the existence of different ecological performances among male morphs (Sinervo et al. 2007). We also found some evidence for an alternative form of inter-cohort competition, namely, social competition (i.e., agonistic social interactions). This latter form of negative density-dependence would have stemmed from differences in the intensity of social interactions, determined by population age and sex structure, and morph frequencies (considering density constant), and proved to be more specific than resource competition, because not all individuals would be necessarily affected (e.g., male-male aggression does not affect females; cannibalism of juveniles by adults does not affect yearlings). In agreement with these results, both types of inter-cohort competition have been reported in previous common lizard studies, where either density or resource abundance (but not climatic variables) was directly manipulated (Massot et al. 1992; Mugabo et al. 2010).

On the other hand, not all environmentally-induced immediate effects could be explained by mechanisms of inter-cohort competition. For instance, adults are dominant over yearlings and juveniles and thus the observed treatment effects on adult growth and survival (chapters I and II) were more likely the result of intra- (not inter-) cohort competition. We cannot disregard the existence of additional effects independent of density contributing to life-history variation, since starting populations were all equal in size and density *per se* was not manipulated (e.g., Bestion et al. 2015). In order to disentangle between strict density-independent effects and density-independent effects acting in interaction with density-dependence, resource availability and climatic conditions would need to be manipulated independently and simultaneously.

Nonetheless, by manipulating climatic conditions and demographic factors we revealed further interactions between density-dependent and density-independent

processes. For example, treatment effects often differed between the sexes. It has long been acknowledged that males and females differ in their life-histories largely due to differences in their reproductive strategies (Trivers 1972). Usually, females compete among themselves for resources such as food, whereas males ultimately compete only for members of the opposite sex. Therefore, it is not surprising that the environment affects the sexes differently, examples of which can be found in species from multiple taxa (Clutton-Brock et al. 1985; Coulson et al. 2001; Wilkin and Sheldon 2009). Male and female common lizards also respond differently to environmental conditions and are believed to be submitted to different selective pressures (Pilorge et al. 1987). However, sex differences have not always been detected in previous experiments despite the existence of a clear sexual dimorphism in growth and adult body size (Le Galliard et al. 2005a; Mugabo et al. 2010). Our results were in line with other studies that indeed found sexual differences in life-history responses to environmental conditions in common lizards (Le Galliard et al. 2010; Massot et al. 1992) and thus supported the existence of different ecological requirements, acquisition or allocation of energy between sexes, and/or differences in the level of social competition experienced by each sex (Mugabo et al. 2011).

Another major determinant of population dynamics is reproduction, since it directly relates to birth rates. In general, we found no immediate differences in female fecundity (clutch size, probability of being gravid) among experimental treatments (chapters I and II). However, the results of chapters III and IV supported the existence of context-dependent mating patterns, with habitat humidity influencing frequency-dependent mate choice. Thus, population structure also affects male competitiveness in terms of reproductive success in this species. This suggests that not only natural selection but also sexual selection are simultaneous acting forces that contribute to shape the dynamics of common lizard populations, and not necessarily in the same direction (e.g., the morph favored by females during mate choice may have an ecological disadvantage in the current environment). The combined effects of both selective pressures thus may influence the persistence of the polymorphism, and the morph composition and frequency in the population has further demographic (chapter I) and evolutionary (McLean and Stuart-Fox 2014) consequences.

Importantly, conditions experienced during early development can also have long-term effects in subsequent life stages or even generations (Metcalfe and Monaghan 2001), and common lizards are no exception (Bleu et al. 2011b; Le Galliard et al. 2005a; Le Galliard et al. 2010; Lindstrom 1999; Mugabo et al. 2011; Mugabo et al.

2011). The here observed immediate effects on different age classes, e.g., on juvenile or yearling growth, may affect future individual performance through trade-offs between growth and future reproduction or between growth and future survival (Le Galliard et al. 2010; Marquis et al. 2008), producing delayed density-dependence with substantial effects on the dynamics of structured populations. Such delayed effects generate lagged responses that frequently increase population variability and may lead to population instability (Beckerman et al. 2002). They may also induce and sustain population oscillations (i.e., cycles; De Roos et al. 2003). In general, patterns of compensation during development (e.g., poor juvenile growth can trade-off with fast yearling growth, Le Galliard et al. 2010) should buffer the demographic consequences of age cohort effects. However, the ability to compensate can also be restrained by inter-cohort interactions in stage-structured populations (Mugabo et al. 2010). Likewise, the conditions experienced by one generation, even during the early stages of life, can cause effects across one, or more generations (Burton and Metcalfe 2014). In chapter I, we showed an example of such trans-generational delayed effects, namely, the effects on offspring size and offspring sex-ratio derived from conditions experienced by the parental generation. Trans-generational effects are also a potential source of lag of density-dependence and increase population variability (Benton et al. 2001). In short, the here presented results strongly supported the well put statement: "the observed life-history is the result of a complex interplay between current conditions, past conditions within the organisms' lifetimes, and the conditions experienced by previous generations" (Benton and Beckerman 2005).

Altogether, the findings of this thesis are in line with the idea that the interplay between density-independent and density-dependent factors are behind life-history trait evolution and population regulation of *Z. vivipara* (Figure 6.1; Pilorge 1981) and highlight the role of demographic structure (whether age or sex classes) and genetic characteristics (morph frequency), not merely density, in density-dependent processes. Given that most natural populations of most species have some kind of stage-structure, similar mechanisms of regulation would be possible in a wide variety of taxa. For example, our results agree with previous population experiments carried out, e.g., with mites (Benton and Beckerman 2005; Benton et al. 2004), water fleas (Drake and Lodge 2004), and field observations of other vertebrates, including birds and mammals (Albon et al. 1987; Clutton-Brock and Coulson 2002; Coulson et al. 2001; Forchhammer et al. 2001; Sæther et al. 2004), where the form of density dependence changed with environmental stochasticity and individuals from different stage classes

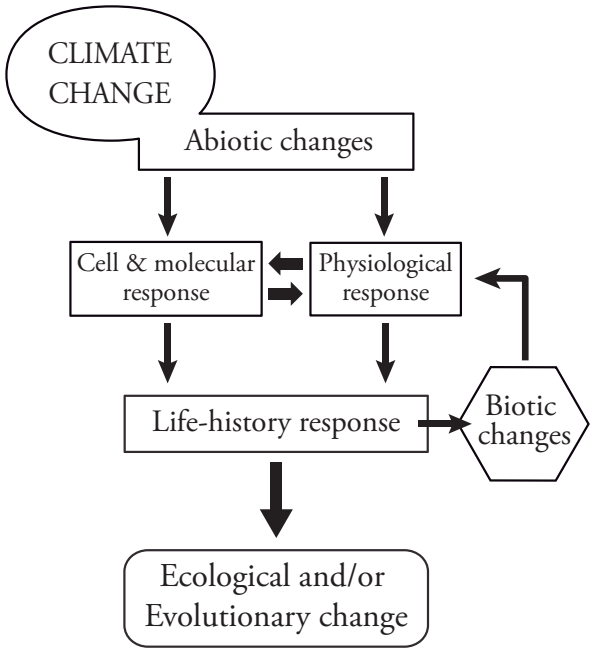


Figure 6.1 Role of climate change, and biological features of organisms (from cell to individual life-history traits) as the determinants of ecological and evolutionary changes at the population level.

responded in different ways to density and climate. Additional experiments, e.g., with butterflies, killifish, and moths (see discussion chapter I and references therein) have suggested that genetic characteristics influence the demographic trajectory of populations. This suggests that the relationship between genotype, phenotype, environment, and population dynamics is not straightforward for most species, that population regulation is more complex than it is often assumed (Benton et al. 2006; Ozgul et al. 2009), and calls for a better understanding of the biology and demographic characteristics of populations at local and regional scales.

Proximate mechanisms

The second main hypothesis of this thesis contemplated that hormones (and thus the endocrine system) are involved in life-history trade-offs, and could mediate plastic adaptive responses following an environmental change. We focused on the stress response and the glucocorticoid hormone corticosterone for its key role in the maintenance of an organism's homeostasis and its ubiquity across the phylogeny. Our results suggested that a mediation role of corticosterone is very likely, since we evidenced a change in mating behavior that translated into a fitness difference as a result of a change in the organism's hormone levels (chapter IV).

Unpredicted environmental changes have repeatedly shown to trigger stress responses (Wingfield 2013), and the physiological components of the stress response act as mediators to produce a range of phenotypes from the same genotype in, e.g., behavior. Such behavioral changes may explain some context-dependent mating strategies, where the experienced environment would serve as a cue, triggering a physiological stress response that allows the individual to adjust its phenotype in heterogeneous environments (Wingfield 2013). For example, when habitat conditions affect behavior (e.g., female choice, chapter III), this process might be mediated by changes in hormone levels in response to the environment. Extrinsic stressors, including agonistic intra- or inter-specific interactions, infection, wounding, and at a greater scale, population density and weather (Summers and Norman 1988; Wingfield 2003) have shown to trigger rapid responses with acute glucocorticoid secretion (Wingfield and Kitaysky 2002) in numerous species (Cash and Holberton 2005; Jessop et al. 2000; Wingfield 1983; Wingfield 2003). These responses may have consequences on sexual conflict (chapter IV), the opportunity and intensity of sexual selection (Hall et al. 2008), the offspring (De Fraipont et al. 2000a; Meylan and Clobert 2005), and thus demography (Meylan et al. 2012). Therefore, the stress response might work as a proximate mechanism in population responses to environmental fluctuations and heterogeneous environments, expressing phenotypic plasticity, and may be one way for coping with global climate change (Meylan et al. 2012; Wingfield 2015).

More detailed studies on the physiology of this and other ancient pathways (e.g., insulin-like growth factor-1 [IGF-1]; Figure 1.3) and their possible interaction are necessary to improve our knowledge on the proximate mechanisms of life-history trade-offs and adaptation (Flatt and Heyland 2011).

Plasticity and adaptation

The use of common lizards gave us an excellent opportunity to evaluate whether the recognized ecological plasticity of this species could serve as a buffer against conditions more or less distant from those preferred. In line with previous studies (Le Galliard et al. 2010; Lorenzon et al. 2001; Mugabo et al. 2010; Sorci et al. 1996a), our results evidenced the flexibility of common lizard's life-history strategy (e.g., on growth rate (chapters I and II), body condition change (chapter I), mating behavior (chapters III and IV), and reproductive investment and timing (chapters I and II) when facing different conditions from both the biotic and abiotic environments. These individual responses were the immediate consequence of the experienced environment and

responses were the immediate consequence of the experienced environment and suggest great adaptive potential via plasticity (Ghalambor et al. 2007), as illustrated e.g., by compensation patterns that allowed overcoming adverse conditions and reaching equal final body sizes and/or fecundity among treatments (chapters I and II). Other delayed compensatory responses may have operated through trans-generational effects that benefited the offspring (chapter I). The latter further suggests that behavioral decisions of mothers, such as choice of mate or oviposition site, besides having important consequences for offspring fitness (Shine 2005), may conceal immense adaptive potential if behavioral changes respond to environmental cues to track environmental fluctuations (Charmantier et al. 2008; Peñalver-Alcázar et al. 2015; Wingfield 2015), especially in species without parental care. Such plasticity may have facilitated the colonization of, and subsequent adaptation to, new habitats throughout the species' phylogeographic history and thus may help explain its wide geographical distribution range.

However, our results also showed that inherent plasticity alone did not suffice to cope *in situ* with all sorts of environmental change, and we found important negative fitness effects such as increased mortality and reduced final body size in adults under increased environmental stochasticity (chapter II), among others. Changes in the biophysical environment and changes in mortality rates are two of the ecological processes that can lead to rapid adaptive evolution (Reznick and Ghalambor 2001). Nevertheless, when plasticity drives the mean phenotype further away from the new local optimum favored by selection (i.e., non-adaptive plasticity), or plasticity is importantly constrained and costly to maintain, the derived population is less likely to persist and plasticity may increase the likelihood of extinction instead of buffering against it (Ghalambor et al. 2007; Snell-Rood et al. 2010). If a population is large enough and only initially mildly maladapted, it might be expected to persist in a novel environment. Conversely, populations that are initially small or severely maladapted will decline to critical sizes sooner and, almost certainly, go extinct. Furthermore, even populations with sufficient genetic capacity to avoid extinction may often fail to do so (Gomulkiewicz and Holt 1995). For common lizards, reduced humidity *per se* did not yield survival differences (chapter I) and perhaps the observed effects on growth rate were part of a trade-off with survival, which would maintain the short-term opportunity for population growth and thus grant better prospects of population recovery. There are yet to be explored the phenotypic consequences that may derive from this abiotic change such as trends and changes in population mean body size over

the following years (Ozgul et al. 2009). Under increased humidity stochasticity, however, there were high survival costs (chapter II) that can immediately affect population size and disrupt population structure. These effects would reduce the short-term opportunity for population growth, hence recovery, after such a climatic change, and reduce the chance of population persistence (Reznick and Ghalambor 2001; see also discussion in chapter II).

Numerous studies on the consequences of climate change have paid more attention to changes in mean values than to fluctuations of climatic variables, even though both factors are predicted by future scenarios of climate change. However, environmental variability has proven to be an important selective factor (Folguera et al. 2011) and studies that only incorporate mean values could present significant limitations when predicting the life-history, ecological and evolutionary impact of climate change. Without going any further, in the present thesis we have shown (chapters I and II, see above) how environmental stochasticity of humidity conditions had more drastic fitness consequences than changes in mean amount of humidity. This calls for not underestimating the role of environmental variability in the persistence of species. For example, in many reptile populations living in environments where resources are scarce or highly variable, the timing of reproduction is adjusted to the sporadic availability of resources (Shine 2005). Here, mean values are not particularly relevant, but bursts of food resources may be followed by bursts of reproductive output, creating huge temporal variance in population size and age structure within the population. Highly fluctuating populations show increased probability of extinction, and decreased average time to extinction (Drake and Lodge 2004; Tuljapurkar and Orzack 1980).

Considerations for conservation and final remarks

Due to ectothermy, the common lizard shares a number of characteristics with other species like insects, fish and amphibians. As a rule, ectotherms have lower metabolic rates than endotherms at a given body mass and thus rely on the environment and their own behavioral patterns to control their temperature. This dependence on ambient conditions to reach operational body temperatures has shaped the lifestyles (including activity and behavior) of many species and it is precisely what makes them more vulnerable to rapid environmental change.

Reptiles and amphibians have perhaps more similarities than any other two groups, and are collectively known as herpetofauna. They occupy similar habitats and are just as vulnerable to habitat degradation. The herpetofauna is actually one of the most

diverse groups of vertebrates in Europe (151 spp. of reptiles, 85 spp. of amphibians) and is also among the most threatened. One fifth of Europe's reptiles (19.4%) and nearly a quarter (22.9%) of its amphibians are threatened (i.e., either "critically endangered", "endangered" or "vulnerable") according to the IUCN (Cox and Temple 2009a; Cox and Temple 2009b), compared to a 15% of mammals and a 13% of birds (BirdLife International 2015; Temple and Terry 2007), which means that "herptiles" are more at risk than mammals and birds. Alarmingly, more than half of all amphibians (59 %) and 42% of reptiles are in decline and, in many cases, the lack of data precludes the comprehensive evaluation of the conservation status of these species in different biogeographical regions (Report from the Commission to the Council and the European Parliament 2015). The great majority of terrestrial European reptiles are members of the order Squamata, and the richest (i.e., most diverse) family is the Lacertidae (with a 29.7% of species threatened), to which *Z. vivipara* belongs.

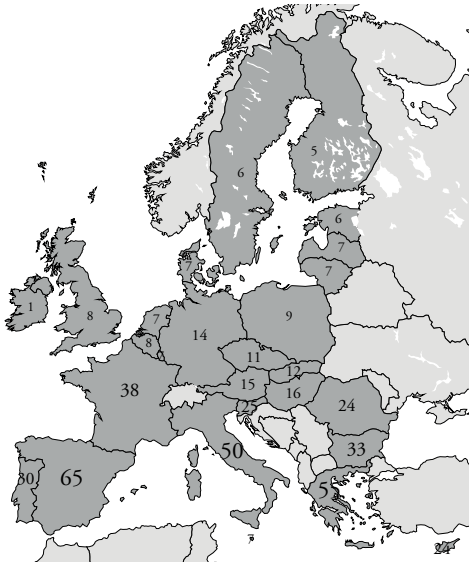


Figure 6.2 Reptile species richness (numbers) in the 27 EU member states (in dark grey). Data from Cox and Temple (2009b).

The above considerations give sufficient reasons of concern regarding the impact of climatic change in the conservation of herptile populations and European biodiversity and emphasize the value of the experiments presented in this thesis. The most important mechanism for population persistence is to shift the geographic distribution in response to long-term climatic alterations. However, the idiosyncrasies of many species and the increasing levels of habitat destruction and fragmentation severely restrict dispersal (Lande 1998) and thus it is likely that numerous species will be forced to face environmental change *in situ*. Using current modeling techniques with conservative (consensus or averaged) projections based on limited dispersal, most European amphibians and reptiles are projected to lose range, following the loss of suitable climate space, especially in the south-west of Europe (Araújo et al. 2006). Reptile biodiversity increases from north to south in Europe (Figure 6.2), which means that important areas of species richness will be affected. According to that study, the

availability) and warmth, particularly for amphibians, although no causal evidences exist. In general terms, our experimental results supported that water availability can constitute an important limiting factor for land reptile species and suggest that reduced habitat humidity and increased stochasticity of habitat humidity (e.g., higher risk of drought) can indeed act as a proximate mechanism of population decline. Additionally, it has been recently shown in an experimental setting that warmer temperature (2°C on average) increases population extinction risk in *Z. vivipara* (Bestion et al. 2015) and thus cumulative effects (synergisms) between humidity and temperature may exacerbate the negative consequences of abiotic changes. Likewise, other major threats not considered in our population experiments, such as habitat loss, degradation and fragmentation, and inter-specific interactions (e.g., predation, parasites) could importantly contribute to population decline independently or interactively with climatic change (Cahill et al. 2013). We must remember, however, that population trends may vary locally according to the demographic structure or genetic characteristics of the population and population size. In this regard, demographic stochasticity in small populations and metapopulation dynamics (e.g., population connectivity, migration, number of neighboring populations) can play important roles in the stability and persistence of populations (Hanski and Gaggiotti 2004).

Finally, even though the common lizard is a relatively well studied species, the diversity of niches that it occupies across its distribution, and inter-population variability (e.g., on demography, reproductive mode, life-history, genetics; Heulin et al. 1997; Horváthová et al. 2013; Sinervo et al. 2007; Surget-Groba et al. 2006) make comparisons and studies in different geographical regions necessary. Less frequently analyzed taxa/species will need considerably higher and pressing efforts (Pacifici et al. 2015), especially those and there where the conservation status is currently unknown.

Conclusions

1 Density-dependent mechanisms are key processes in the dynamics of *Z. vivipara* populations, specifically, asymmetric inter-cohort competition between the adult and younger age classes and intra-cohort competition among adults. Inter-individual competition may have an ecological or a social basis.

2 Exogenous factors, habitat humidity and precipitation stochasticity, importantly interact with endogenous factors, namely population age, sex and morph composition, affecting density-dependent regulation. Ultimately, it is this interplay between both types of factors that affects population dynamics of *Z. vivipara*.

3 Individual *Z. vivipara* life-history strategy (i.e., growth and reproductive traits) is affected by immediate and delayed—either trans-stage or trans-generational—effects of density-dependent and density-independent processes, which are mediated through a number of trade-offs. In turn, individual life histories determine demographic rates and the dynamic of the population.

4 There exists a pattern of context-dependent mating in which female mate choice depends mainly on the current yearling morph frequencies. This process is influenced, at least, by habitat humidity and determines male competitiveness in terms of siring success of recruited progeny. Consequently, genetic characteristics (i.e., morph composition and frequency) are key determinants of sexual selection in *Z. vivipara*.

5 The suggested ecological differences among morphs reinforce the idea that morph composition is important in population dynamics of *Z. vivipara* and, together with the above conclusion, suggest that both natural and sexual selection are co-acting forces driving population dynamics, and are responsible for the maintenance of the color polymorphism.

6 Given that exogenous and endogenous factors can trigger physiological responses that affect the level of glucocorticoids such as corticosterone, these may alter the strength of sexual selection, the sexual conflict and, in this way, the dynamics of *Z. vivipara* populations. This makes corticosterone a plausible mediator in processes of plasticity and adaptation in response to environmental change.

7 Despite *Z. vivipara* demonstrates flexibility in life-history traits that allow certain degree of compensation, facing environmental abiotic changes predicted by scenarios of climate change *in situ* can have large negative fitness effects that

would compromise the viability of populations. The capacity to respond, recover and persist will importantly depend on local demographic characteristics (e.g., population size and structure).

8 Climatic stochasticity could sometimes have more drastic fitness consequences than changes in mean values in climatic components and it would be advisable to take it into account. Increasing population fluctuation also increases the probability of extinction.

9 Our results in *Z. vivipara* agree with the projected range losses in European reptiles and amphibians under future scenarios of climate change, demonstrating that changes in environmental humidity can be a proximate mechanism through which climate change will lead to population decline and loss of biodiversity.

Conclusiones

1 Los mecanismos dependientes de la densidad son procesos clave para la dinámica de poblaciones en *Z. vivipara*, en concreto, la competencia asimétrica entre las clases de edad adulta y otras más jóvenes y la competencia intra-cohorte entre los adultos. La competencia entre individuos puede ser de naturaleza ecológica o social.

2 Los factores exógenos, humedad de hábitat y estocasticidad de las precipitaciones, interactúan de manera importante con factores endógenos, es decir, con las estructuras de edad, sexo y composición de morfos en la población, afectando a la regulación dependiente de la densidad. Al final, es esta interacción entre ambos tipos de factores lo que rige la dinámica poblacional de *Z. vivipara*.

3 La estrategia individual en la historia de vida en *Z. vivipara* (i.e., rasgos de crecimiento y reproductivos) se ve afectada por efectos inmediatos y retrasados—ya sean trans-etapa o trans-generacionales—de procesos denso-dependientes e -independientes, mediados por una serie de trade-offs. A su vez, las historias de vida individuales determinan las tasas demográficas y la dinámica de la población.

4 Existe un patrón de apareamiento dependiente del contexto por el cual la elección de pareja por parte de la hembra depende principalmente de las frecuencias actuales de morfos en los subadultos. Este proceso está influenciado, al menos, por la humedad del hábitat y determina la competitividad de los machos en términos de éxito reproductivo y reclutamiento de su progenie. En consecuencia, la estructura de la población (i.e., la composición y frecuencia de morfos) es un determinante clave de la selección sexual en *Z. vivipara*.

5 Las aparentes diferencias ecológicas entre morfos refuerzan la idea de que la estructura de morfos es importante para la dinámica de poblaciones de *Z. vivipara* y, junto con la conclusión anterior, sugieren que tanto la selección natural como la selección sexual son fuerzas que co-actúan, dirigiendo la dinámica poblacional y son las responsables del mantenimiento del polimorfismo.

6 Dado que factores exógenos y endógenos pueden afectar a los niveles de glucocorticoides, como la corticosterona, éstos podrían alterar directamente la fuerza de la selección sexual, el conflicto sexual y así a la dinámica poblacional de *Z. vivipara*, convirtiendo a esta hormona en un mediador apropiado/probable en procesos de plasticidad y adaptación en respuesta a cambios ambientales.

7 A pesar de que *Z. vivipara* demuestra flexibilidad en varios rasgos de historia de vida que le permiten cierto grado de compensación/adaptabilidad, enfrentarse *in situ* a cambios abióticos ambientales previstos en los escenarios sobre cambio climático puede tener grandes efectos negativos sobre la eficacia biológica que comprometerían la viabilidad de sus poblaciones. La capacidad de responder, recuperar y persistir dependerá en gran medida de las características demográficas a nivel local (e.g., tamaño y estructura de la población).

8 La estocasticidad climática a veces podría tener consecuencias más drásticas sobre la eficacia biológica que los cambios en valores medios de los componentes climáticos y sería recomendable tenerla en cuenta. El aumento de la fluctuación poblacional también aumenta la probabilidad de extinción.

9 Nuestros resultados sobre *Z. vivipara* están de acuerdo con la disminución del rango de expansión proyectado por los modelos para los reptiles y anfibios europeos bajo escenarios futuros de cambio climático. Esto demuestra que los cambios en la humedad ambiental pueden ser un mecanismo próximo a través del cual el cambio climático conducirá a la disminución de las poblaciones y a la pérdida de biodiversidad.

References

Albon, S. D., T. H. Cluttonbrock, and F. E. Guinness. 1987. Early development and population-dynamics in red deer. II. Density-independent effects and cohort variation. Journal of Animal Ecology 56:69-81.

Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712–1728.

Avery, R. A. 1966. Food and feeding habits of common lizard (*Lacerta vivipara*) in west of England. Journal of Zoology 149:115-&.

Beckerman, A. P., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology & Evolution 17:263-269.

Benton, T. G., and A. P. Beckerman. 2005. Population dynamics in a noisy world: Lessons from a mite experimental system, Pages 143-181 Advances in Ecological Research, Academic Press.

Benton, T. G., T. C. Cameron, and A. Grant. 2004. Population responses to perturbations: predictions and responses from laboratory mite populations. Journal of Animal Ecology 73:983-995.

Benton, T. G., S. J. Plaistow, and T. N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B: Biological Sciences 273:1173-1181.

Benton, T. G., E. Ranta, V. Kaitala, and A. P. Beckerman. 2001. Maternal effects and the stability of population dynamics in noisy environments. Journal of Animal Ecology 70:590-599.

Bestion, E., A. Teyssier, M. Richard, J. Clobert, and J. Cote. 2015. Live fast, die young: Experimental evidence of population extinction risk due to climate change. PLoS Biology 13:e1002281.

BirdLife International. 2015. European red list of birds, Luxemburg: Office for Official Publications of the European Communities.

Bleu, J., M. Massot, C. Haussy, and S. Meylan. 2011b. Experimental litter size reduction reveals costs of gestation and delayed effects on offspring in a viviparous lizard. Proceedings of the Royal Society B: Biological Sciences 279:489-498.

Burton, T., and N. B. Metcalfe. 2014. Can environmental conditions experienced in early life influence future generations? Proceedings of the Royal Society B: Biological Sciences 281.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Yeong Ryu, G. C. Sbeglia et al. 2013. How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences 280.

Cash, W. B., and R. L. Holberton. 2005. Endocrine and behavioral response to a decline in habitat quality: effects of pond drying on the slider turtle, *Trachemys scripta*. Journal of Experimental Zoology Part A: Comparative Experimental Biology 303A:872-879.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131-133.

Clutton-Brock, T. H., and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1285-1298.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley et al. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528-1531.

Cox, N. A., and H. J. Temple. 2009a. European red list of amphibians, Luxembourg: Office for Official Publications of the European Communities.

—. 2009b. European red list of reptiles, Luxembourg: Office for Official Publications of the European Communities.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800-803.

Chikoski, J. M., S. H. Ferguson, and L. Meyer. 2006. Effects of water addition on soil arthropods and soil characteristics in a precipitation-limited environment. Acta Oecologica-International Journal of Ecology 30:203-211.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond Predictions: Biodiversity conservation in a changing climate. Science 332:53-58.

De Fraipont, M., J. Clobert, H. John-Alder, and S. Meylan. 2000a. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. Journal of Animal Ecology 69:404-413.

De Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473-487.

Drake, J. M., and D. M. Lodge. 2004. Effects of environmental variation on extinction and establishment. Ecology Letters 7:26-30.

Flatt, T., and A. Heyland. 2011. Mechanisms of life history evolution: The genetics and physiology of life history traits and trade-offs, Oxford University Press.

Forchhammer, M. C., T. H. Clutton-Brock, J. Lindstrom, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70:721-729.

Ghalambor, C. K., J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21:394-407.

Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural selection prevent extinction. Evolution 49:201-207.

Hall, M. D., L. F. Bussiere, J. Hunt, and R. Brooks. 2008. Experimental evidence that sexual conflict influences the opportunity, form and intensity of sexual selection. Evolution 62:2305-2315.

Hanski, I., and O. E. Gaggiotti. 2004, Ecology, genetics, and evolution of metapopulations, Elsevier Academic Press.

Heulin, B., K. Osenegg-Leconte, and D. Michel. 1997. Demography of a bimodal reproductive species of lizard (*Lacerta vivipara*): Survival and density characteristics of oviparous populations. Herpetologica 53:432-444.

Horváthová, T., C. Cooney, R., P. Fitze, S., T. Oksanen, A., D. Jelić, I. Ghira, T. Uller et al. 2013. Length of activity season drives geographic variation in body size of a widely distributed lizard. Ecology and Evolution 3:2424–2442.

Jessop, T. S., M. Hamann, M. A. Read, and C. J. Limpus. 2000. Evidence for a hormonal tactic maximizing green turtle reproduction in response to a pervasive ecological stressor. General and Comparative Endocrinology 118:407-417.

Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. Researches on Population Ecology 40:259-269.

Le Galliard, J.-F., R. Ferriere, and J. Clobert. 2005a. Juvenile growth and survival under dietary restriction: are males and females equal? Oikos 111:368-376.

Le Galliard, J.-F., O. Marquis, and M. Massot. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. Journal of Animal Ecology 79:1296-1307.

Lindstrom, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology & Evolution 14:343-348.

Lorenzon, P., J. Clobert, and M. Massot. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. Evolution 55:392-404.

Marquis, O., M. Massot, and J.-F. Le Galliard. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. Ecology 89:2575-2583.

Massot, M., J. Clobert, T. Pilorge, J. Lecomte, and R. Barbault. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. Ecology 73:1742-1756.

McLean, C. A., and D. Stuart-Fox. 2014. Geographic variation in animal colour polymorphisms and its role in speciation. Biological reviews of the Cambridge Philosophical Society 89:860-873.

Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology & Evolution 16:254-260.

Meylan, S., and J. Clobert. 2005. Is corticosterone-mediated phenotype development adaptive? Maternal corticosterone treatment enhances survival in male lizards. Hormones and Behavior 48:44-52.

Meylan, S., D. B. Miles, and J. Clobert. 2012. Hormonally mediated maternal effects, individual strategy and global change. Philosophical Transactions of the Royal Society of London B: Biological Sciences 367:1647-1664.

Mugabo, M., O. Marquis, S. Perret, and J.-F. Le Galliard. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. Journal of Evolutionary Biology 23:1886 - 1898.

—. 2011. Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. Oecologia.

Ozgul, A., S. Tuljapurkar, T. G. Benton, J. M. Pemberton, T. H. Clutton-Brock, and T. Coulson. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. Science 325:464-467.

Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R. Scheffers et al. 2015. Assessing species vulnerability to climate change. Nature Climate Change 5:215-224.

Peñalver-Alcázar, M., C. Romero-Diaz, and P. S. Fitze. 2015. Communal egg-laying in oviparous *Zootoca vivipara louislantzi* of the Central Pyrenees. Herpetology Notes 8:4-7.

Pilorge, T. 1981. Structure et dynarnique d'une population du lézard vivipare. Signification adaptive de la viviparité chez les lézards. Bulletin de la Societé Herpetologique de France 18:29-31.

Pilorge, T., J. Clobert, M. Massot, J. J. van Gelder, H. Strijbosch, and P. J. M. Bergers. 1987. Life history variations according to sex and age in *Lacerta vivipara*, Pages 311-315 Proceedings of the 4th Ordinary General Meeting of the Societas Europaea Herpetologica., Societas Europaea Herpetologica, Faculty of Sciences, Nijmegen.

Report from the Commission to the Council and the European Parliament. 2015. Report on the status of and trends for habitat types and species covered by the Birds and Habitats Directives for the 2007-2012 period as required under Article 17 of the Habitats Directive and Article 12 of the Birds Directive. Luxembourg: Office for Official Publications of the European Union, European Union.

Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: What empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112:183-198.

Sæther, B.-E., W. J. Sutherland, and S. Engen. 2004. Climate influences on avian population dynamics, Pages 185-209 Advances in Ecological Research, Academic Press.

Shine, R. 2005. Life-history evolution in reptiles, Pages 23-46 Annual Review of Ecology Evolution and Systematics. Annual Review of Ecology Evolution and Systematics. Palo Alto, Annual Reviews.

Sinervo, B., B. Heulin, Y. Surget-Groba, J. Clobert, D. B. Miles, A. Corl, A. Chaine et al. 2007. Models of density-dependent genic selection and a new rock-paper-scissors social system. American Naturalist 170:663–680.

Snell-Rood, E. C., J. D. Van Dyken, T. Cruickshank, M. J. Wade, and A. P. Moczek. 2010. Toward a population genetic framework of developmental evolution: The costs, limits, and consequences of phenotypic plasticity. Bioessays 32:71-81.

Sorci, G., J. Clobert, and S. Belichon. 1996a. Phenotypic plasticity of growth and survival in the common lizard *Lacerta vivipara*. Journal of Animal Ecology 65:781-790.

Summers, C. H., and M. F. Norman. 1988. Chronic low humidity-stress in the lizard *Anolis carolinensis*: changes in diurnal corticosterone rhythms. Journal of Experimental Zoology 247:271-278.

Surget-Groba, Y., B. Heulin, C.-P. Guillaume, M. Puky, D. Semenov, V. Orlova, L. Kupriyanova et al. 2006. Multiple origins of viviparity, or reversal from viviparity to oviparity? The European common lizard (*Zootoca vivipara, Lacertidae*) and the evolution of parity. Biological Journal of the Linnean Society 87:1-11.

Temple, H. J., and A. Terry. 2007. The status and distribution of European mammals, Pages viii + 48pp., Luxembourg: Office for Official Publications of the European Communities.

Trivers, R. L. 1972. Parental investment and sexual selection, Pages 136-207 *in* B. Campbell, ed. Sexual Selection and the descent of man 1871-1971. Chicago, Aldine Publishing Company.

Tsiafouli, M. A., A. S. Kallimanis, E. Katana, G. P. Stamou, and S. P. Sgardelis. 2005. Responses of soil microarthropods to experimental short-term manipulations of soil moisture. Applied Soil Ecology 29:17-26.

Tuljapurkar, S. D., and S. H. Orzack. 1980. Population dynamics in variable environments I. Long-run growth rates and extinction. Theoretical Population Biology 18:314-342.

Turchin, P. 1995. Population regulation: Old arguments and a new synthesis, Pages 19-40 *in* N. Cappuccino, and P. W. Price., eds. Population Dynamics: New Applications and Synthesis. NY, Academic Press.

Wilkin, T. A., and B. C. Sheldon. 2009. Sex differences in the persistence of natal environmental effects on life histories. Current Biology 19:1998-2002.

Wingfield, J. C. 1983. Endocrine responses to inclement weather in naturally breeding populations of white-crowned sparrows (*Zonotrichia leucophrys pugetensis*). The Auk 100:56.

–. 2003. Control of behavioural strategies for capricious environments. Animal Behaviour 66:807-815.

–. 2013. Ecological processes and the ecology of stress: the impacts of abiotic environmental factors. Functional Ecology 27:37-44.

–. 2015. Coping with change: A framework for environmental signals and how neuroendocrine pathways might respond. Frontiers in Neuroendocrinology 37:89-96.

Wingfield, J. C., and A. S. Kitaysky. 2002. Endocrine responses to unpredictable environmental events: Stress or anti-stress hormones? Integrative and Comparative Biology 42:600-609.

ANNEX: MATLAB® CODE

BASE MODEL: FREQUENCY-DEPENDENT MATING

The following function code for MATLAB® was used to determine male relative competitiveness, assuming a frequency-dependent mating pattern with asymmetric effects (i.e., model FA). Every other candidate model (Table 4.1) was developed from this base code by adding or replacing input parameters as described in chapter III: "Model development and analysis".

```
% input
abg=[αb αo αy αw βb βo βy βw γb γo γy γw]

% This function: Frequency dependent mating, asymmetric (FA).
function [loglike]=FA (abg,x,hum)
% abg=[alphasbetasgammas], x = relative importance of juveniles,
% hum(idity)='high' or 'low'
lizards; % data table
if nargin < 3; hum = 0; end

% there are 11 enclosures:
enc=[2 3 5 7 8 9 10 11 12 14 15]';

% let's go through all
for i=1:length(enc)

   % initialize all allele frequencies as 0 (no males yet found), then update
   orangeMalleles=[0 0]; % juveniles then adults
   yellowMalleles=[0 0];
   whiteMalleles=[0 0];

   % find juveniles who live here
   f=find(Males(:,enclosure)==enc(i) & Males(:,age)==SubAD);
   orangeMalleles(1)=sum(Males(f,allele1)==o)+sum(Males(f,allele2)==o);
   yellowMalleles(1)=sum(Males(f,allele1)==y)+sum(Males(f,allele2)==y);
   whiteMalleles(1)=sum(Males(f,allele1)==w)+sum(Males(f,allele2)==w);
   % find adults who live here
   f=find(Males(:,enclosure)==enc(i) & Males(:,age)==AD);
   orangeMalleles(2)=sum(Males(f,allele1)==o)+sum(Males(f,allele2)==o);
   yellowMalleles(2)=sum(Males(f,allele1)==y)+sum(Males(f,allele2)==y);
   whiteMalleles(2)=sum(Males(f,allele1)==w)+sum(Males(f,allele2)==w);
   % proportions

s=x*(sum(orangeMalleles(1))+sum(yellowMalleles(1))+sum(whiteMalleles(1)))+...
  (1-x)*(sum(orangeMalleles(2))+sum(yellowMalleles(2))+sum(whiteMalleles(2)));
   po(1)=(x*orangeMalleles(1)+(1-x)*orangeMalleles(2))/s;
   py(1)=(x*yellowMalleles(1)+(1-x)*yellowMalleles(2))/s;
   pw(1)=(x*whiteMalleles(1)+(1-x)*whiteMalleles(2))/s;
   % pw=1-po-py;

   % now consider all the adult individuals in the enclosure to calculate
% their relcomp
    g=find(Males(:,enclosure)==enc(i));

for j=1:length(g)
        % relative competitiveness of this individual, first based on his
% first allele
```

```
        switch Males(g(j),allele1)
            case 1, % orange
                relcomp(g(j))=sum(abg(1:4).*[1 po py pw]);
            case 2, % yellow
                relcomp(g(j))=sum([abg(5),abg(6),abg(7),abg(8)].*[1 po py
pw]);
            case 3, % white
                relcomp(g(j))=sum([abg(9),abg(10),abg(11),abg(12)].*[1 po py
pw]);
        end
        % then add the other allele
        switch Males(g(j),allele2)
            case 1, % orange
                relcomp(g(j))=relcomp(g(j))+sum(abg(1:4).*[1 po py pw]);
            case 2, % yellow

relcomp(g(j))=relcomp(g(j))+sum([abg(5),abg(6),abg(7),abg(8)].*[1 po py pw]);
            case 3, % white

relcomp(g(j))=relcomp(g(j))+sum([abg(9),abg(10),abg(11),abg(12)].*[1 po py
pw]);
        end
    end
    % now zero-sum conditions for everyone in this group, i.e. relcomp must
    % sum up to 1 within each enclosure
    rs=sum(exp(relcomp(g)));
    Relcomp(Males(g,indivID))=exp(relcomp(g))/rs;

end
Relcomp=Relcomp(:);

if strcmp(hum,'high')
    loglike=sum(log(Relcomp(Juv(Juv(:,humidity)==H,FatherID)))) % Only
% considering juveniles that survived to contribute to next generation
  elseif strcmp(hum,'low')
    loglike=sum(log(Relcomp(Juv(Juv(:,humidity)==L,FatherID))))
  else
    loglike=sum(log(Relcomp(Juv(Juv(:,survived)==1,FatherID)))); % always keep
end
```

The following code corresponds to the optimization function that estimated the best value of *x* and AIC for each model (the example below is for the 'FA' model).

```
accuracy=100;
xvalues=linspace(0,0.99999,accuracy); LogLike=NaN*xvalues;
inputs=[αb αo αy αw βb βo βy βw γb γo γy γw]; %change input as convenient
for i=1:length(xvalues)
    [y,loglike]= fminsearch(@(y)-FA(y,xvalues(i)),inputs);
    LogLike(i)=-loglike;
end
figure(1); plot(xvalues,LogLike,'o-')
[BestLogLike,whichone]=max(LogLike);
BestX=xvalues(whichone);

% calculate AIC. Parameter numbers = input length PLUS ONE whenever the best x
% is computed, not fixed.
AIC=-2*BestLogLike+2*(length(inputs)+1);
% Recalculate AIC using the best estimated x value as input
```